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RESEARCH ARTICLE

Biohybrid Superorganisms—On the Design of a Robotic System for Thermal Interactions With Honeybee Colonies

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ABSTRACT Social insects, such as ants, termites, and honeybees, have evolved sophisticated societies where collaboration and division of labor enhance survival of the whole colony, and are thus considered “superorganisms”. Historically, studying behaviors involving large groups under natural conditions posed significant challenges, often leading to experiments with a limited number of organisms under artificial laboratory conditions that incompletely reflected the animals’ natural habitat. A promising approach to exploring animal behaviors, beyond observation, is using robotics that produce stimuli to interact with the animals. However, their application has predominantly been constrained to small groups in laboratory conditions. Here we present the design choices and development of a biocompatible robotic system intended to integrate with complete honeybee colonies in the field, enabling exploration of their collective thermoregulatory behaviors via arrays of thermal sensors and actuators. We tested the system’s ability to capture the spatiotemporal signatures of two key collective behaviors. A 121-day observation revealed thermoregulation activity of the broodnest area during the foraging season, followed by clustering behavior during winter. Then we demonstrated the system’s ability to influence the colony by guiding a cluster of bees along an unnatural trajectory, via localized thermal stimuli emitted by two robotic frames. These results showcase a system with the capability to experimentally modulate honeybee colonies from within, as well as to unobtrusively observe their dynamics over extended periods. Such biohybrid systems uniting complete societies of thousands of animals and interactive robots can be used to confirm or challenge the existing understanding of complex animal collectives.

INDEX TERMS Animal-robot interaction, biohybrid, honeybee, insect, interactive robotics, mixed-society, robot, superorganism.

I. INTRODUCTION

With a brain merely the size of a small grain of sand (1 mm^3), honeybees nevertheless demonstrate complex behaviors [1], [2]. Honeybee colonies function as a superorganism [3], a collective entity shaped through natural selection at the colony level, guiding individual members to operate in a coordinated

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manner, akin to the cells or organs in a body. The cooperation between individuals increases the chances of reproduction and survival [4]. For instance, these collaborations can be seen in collective behaviors, where a group is more efficient than a solitary individual. Such collective behaviors are often interpreted to be “swarm-intelligent” behaviors, arising as emergent effects of many interacting individual behaviors. These mechanisms are not only interesting for understanding natural swarm systems, but often also sources

of inspiration for novel technological manifestations of these principles [5]. Examples of highly relevant collective behaviors are diverse within honeybees, most notably in their foraging decision-making [6] and in their thermoregulatory behaviors [7], or in various mechanisms of division of labor by task specialization [8]. Interestingly, these collective behaviors mostly emerge without any leader or orchestrator, making superorganisms (colonies) prominent self-organized biological systems [9], [10], [11], which are fertile ground for intriguing research questions. Several still unanswered questions are: how do such colonies achieve highly sophisticated behavioral patterns and collaborate towards specific goals? How is this capability based on the information flows inside the community? Which communication pathways are relevant to achieve the observed collective decision-making?

However, investigating collective behaviors within densely populated colonies presents inherent challenges often leading to experiments of limited duration or conducted in settings that deviate significantly from the animals' natural conditions. A modern approach to investigating these intriguing collective dynamics that addresses some of these difficulties involves creating biohybrid societies in which artificial agents (robots) collaborate with natural agents (animals) [12], [13]. Through the establishment of an interaction pathway between these two distinct entities [14], researchers can explore the intricacies of collective intelligence, communication, and the emergence of complex behaviors in superorganism colonies.

Our aim is to develop a biohybrid society for studying collective thermoregulatory behaviors of the honeybee. To achieve this objective, we developed a biocompatible robot that can be embedded within a bee colony, and is capable of sensing and generating thermal stimuli over timescales that match these long-running behaviors of interest. The purpose of this paper is to present a detailed technical perspective on the development and validation of this robotic system.

A. CHALLENGES IN STUDYING SOCIAL ANIMALS

One of the main challenges of studying honeybee societies, and in fact most social animals, lies in the difficulty of emulating an appropriate social context where group-living animals can be investigated without overly disturbing their natural behavior. Experiments in environments that differ significantly from their natural habitats might miss vital biotic and abiotic cues, like pheromones or light conditions, essential for influencing their group dynamics. Additionally, using only a small number of animals, due to experimental apparatus constraints, can also bias results since individual behaviors often depend on interactions with nestmates [13]. Moreover, classes of animal behaviors can unfold over different temporal patterns, indicating the need for multi-timescale studies [15], [16]. If specific behaviors require observations or interactions to be performed at short intervals, or over very long time spans, certain studies might be infea-

sible in setups lacking the required sophistication. Lastly, investigating complex behaviors might require a closed-loop interaction sequence, where the subsequent stimuli depend on an animal's response to preceding ones. Achieving this dynamic interplay using traditional techniques, where states or parameters are manually adjusted, might be impractical [17].

B. ROBOTICS IN BEHAVIORAL BIOLOGY

The use of robots that interact with animals is a recent methodology for behavioral biology, or ethology, that attempts to overcome some of the above challenges [14]. Modern robotics, bolstered by advances in technology, can actuate quickly, can sense a wide range of variables, can track multiple parameters at high rates, can be programmed to execute sequences of actions at many levels of complexity, and tirelessly perform repetitive tasks. Historically, ethological research has embraced pioneering techniques, setting the stage for contemporary interactive robotic studies in social animal research [20]. A notable early study by Nobel Prize laureate Nikolaas Tinbergen in 1950 employed a simple lure to investigate the feeding behavior of the herring gull [21], seeding the approach of presenting stimuli to animals with idealized mimics. Fast forward a few decades, the use of robotics in behavioral studies, inspired by this approach, expanded. For instance, Michelsen et al. utilized a mechanical honeybee mimic, which performed 15 Hz lateral oscillations in a repeating loop, in an attempt to decipher the intricacies of the waggle dance communication [22]. Similarly, Halloy et al. introduced autonomous robots into cockroach groups, and intriguingly, the insects perceived these robots as their kin [12], finding that the behavioral program of the robots, and inclusion of pheromones were key to enable the investigation.

While robotics in behavioral biology might seem nascent, a growing body of research showcases successful robotic integrations in experiments. For example, a "cyborg" approach, where electrodes are inserted into the animal's nervous system, has been used to study insect locomotion, such as beetles [23] and locusts [24], as well as robotic navigation using an animal's sensory apparatus such as antennae of moths [25]. An alternative approach, central to robotics investigating social interactions, is to present stimuli externally, that is, in a non-invasive manner. Robotics have been developed to interact with a variety of species, including vertebrates such as ducks [26], chickens [27], frogs [28], electric fish [29], zebrafish [30], [31], and rummy-nose tetra fish [32]; and invertebrates such as cockroaches [12], ants [33], stag beetles [34], crickets [35], flies [36], [37], and honeybees [22], [38], [39], [40], [41], [42], [43], underscoring the transformative potential of robotics in the domain [44]. Examining the results obtained with robotics that interact with honeybees more closely, the works have covered several important social behaviors using a variety of cues. These include: investigating the waggle dance by



FIGURE 1. A robotic system to interact with honeybee thermoregulatory behaviors. (a) A beekeeper inspects a robotic frame installed in a hive. (b) An important collective behavior, the winter cluster, forms when the colony experiences low temperatures. (c) Horizontal thermal profile transecting the middle of the cluster, indicating “safe” temperatures near the center of the cluster and temperatures close to the ambient at the extremities of the frame. (d) Close-up of a broodnest section, with larvae visible at the edge of the capped cells. (e) In the foraging season, broodnest temperatures stay within 33 °C to 36 °C [18], [19]. The graph contrasts the tight regulation of a specific brood region (black dots) against ambient temperature fluctuations (blue curve). Note: temperature graphs do not correspond to the photographed colonies.

mimicking its motion and incorporating additional cues such as wing flapping [22], [41]; information exchange between different species [42] to examine the possibility of

coordinating collective decisions; honeybees’ responses to thermal cues, in small groups of young worker bees [38], [39], and within intact colonies during the winter [40]; and

the potential for aggregating small groups of bees with vibrational cues, generated by a distributed set of static robots [39], [43].

Generally, such robot-animal interaction relies on the robotic elements generating cues or signals that are perceived by the animals and consequently have a modulating effect on the animal behavior. It is essential to identify an appropriate interaction pathway to ensure that the generated stimuli suit the specific organism and behavior being studied [14]. For example, to stimulate motion, two common approaches are the use of miniature mobile robots [12], [34], [35], and gantry-style setups that move a lure in a constrained space [22], [33], [41], which may be hidden from view [36]. Many different factors have been used in investigations by robots, including visual appearance [32], [45], [46], auditory signals [27], [28], substrate-born vibrations [43], odors [12], [33], [34], [35], [36], or thermal cues, as employed in studies with honeybees.

The studies mentioned have contributed to ethology using robotic systems. However, it is important to note that the majority of these investigations have been conducted under laboratory conditions, involving small numbers of animals and over relatively limited timescales. Robots have been deployed in natural habitats to observe animal behaviors on land [47], in water [48], and in the air [49], [50]. These studies were primarily focused on passive observation, aiming to minimize disturbances to animal behavior through techniques such as camouflage [47] and biomimicry [48]. While this approach addresses the limitations of artificial environments and small group sizes, it does not attempt to generate any stimuli to interact with animals or deliberately induce specific behaviors.

C. COLLECTIVE THERMOREGULATION IN HONEYBEES

Honeybees continually engage in a set of collective thermoregulatory behaviors vital for the colony's survival [18]. Honeybees have developed efficient strategies to regulate the thermal conditions of their nest in various scenarios. Unlike most insects that hibernate during winter in temperate climates, honeybee colonies remain active within the hive [51]. When ambient temperatures are low, the colony forms a cohesive self-organized “winter cluster” to produce and sustain temperatures at safe levels, optimizing the use of the limited stores collected during the warmer months (Fig. 1b) [52]. With the onset of the foraging season, marked by warmer temperatures and longer daylight, the queen begins laying up to 2000 eggs per day [53] to produce the next generation of workers and drones [54]. The cells filled with eggs form the broodnest, which requires a strictly regulated temperature for the healthy development of the bees [19], [55], [56]. Throughout the developmental stages of the brood worker bees maintain broodnest homeostasis, sometimes raising temperatures through metabolic heat produced by activating their flight muscles without moving their wings [51] or cooling the brood areas [57], [58].

D. CONTRIBUTIONS

Despite the vast efforts to date, many gaps remain in the knowledge of thermoregulation in insects [59]. The integration of robotic systems into animal colonies may provide a new approach to studying collective thermoregulation: By using robotic systems aiming to generate stimuli that the animals perceive as signals from their own colony members, we could enable a more controlled, detailed observation of responses over long timescales.

In this work, we detail the design and validation of an interactive robotic system tailored to study the collective thermoregulatory behaviors of honeybee colonies from within their hives. Drawing inspiration from recent methodologies [14], [60], we devised a stationary robotic system capable of mixing with complete honeybee colonies and compatible with scientific and agricultural hives (Fig. 1). After empirically characterizing the sensing and actuation functionalities of the system (Sec. II), we performed two experiments with animal groups (Sec. III). The first experiment confirmed the system's capability to provide high-fidelity observations of thermoregulatory behaviors during warm and cold seasons. The second experiment validated the thermal actuators' capabilities to modulate the collective position of thousands of bees. The system was previously presented in the context of research on winter clusters [40]. In contrast, the current paper presents a technical perspective on the design choices and the development process, resulting in a biocompatible tool. Here, we provide new experimental results that characterize the system performance and illustrate its functionality for investigating thermoregulation over extended periods of time. The experiments with complete colonies demonstrate that the robotic system is a versatile tool applicable in multiple seasons such as investigating the broodnest in summer, and clustering in winter. These results reveal the potential of the biohybrid robotic system in future studies to confirm or challenge existing understanding in collective thermobiology.

The remainder of the paper is structured as follows: Section II presents the specification and detailed design of the robotic system. It also provides characterization data for the sensor and actuator subsystems. Section III presents experimental results involving complete animal colonies. Section IV discusses the system and results in a broader context. Finally, Section V provides methodological details on animals and collecting and processing experimental data.

II. THE DESIGN OF AN INTERACTIVE ROBOTIC SYSTEM TO EXPLORE HONEYBEE THERMOBIOLOGY

Collective behaviors within a bee colony predominantly occur inside the hive [8], making their systematic and non-disruptive study challenging. In this section, we outline the design, construction, and characterization of a robotic device tailored to integrate into a honeybee colony and interact with their collective thermoregulatory behaviors. We elaborate on the system's overall architecture, its sensing and modulatory functionalities, and the mechanical

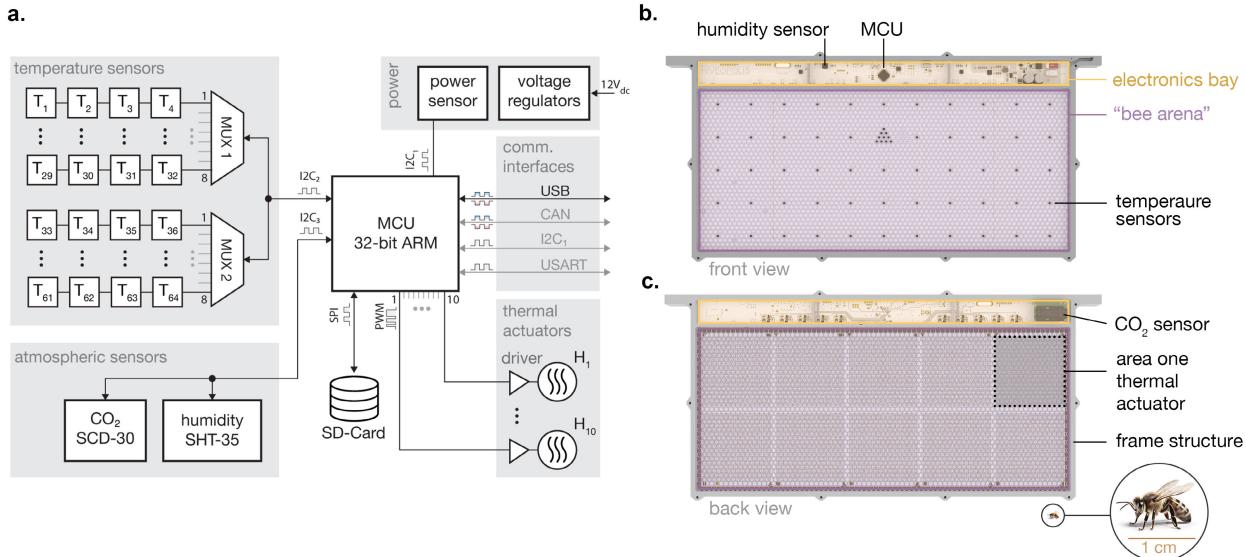


FIGURE 2. System architecture and principal components. (a) System organization with its main building blocks. (b, c) The location of the main parts of the system in a 3D representation of the robotic frame. The orange zone indicates a portion of the frame, inaccessible to bees, dedicated to hosting most electronic parts of the system (excluding the temperature sensors). The purple zone is allocated as space for bee occupancy, such as for comb construction. The shape of the system is discussed in Sec. II-D.

construction ensuring compatibility with both agricultural and scientific hives. Finally, we describe the adopted procedures to prepare the system for animal integration.

A. SYSTEM ARCHITECTURE

A device intended to form a mixed society with living animals must, like most robots, possess sensing and actuating capabilities complemented by some computational power [14], [61]. Our system embodies these three elements, as illustrated in Fig. 2a. At its core a 32-bit microcontroller unit (MCU, STMicroelectronics STM32F405) orchestrates the system, gathering data from sensors, managing thermal actuators, and communicating with external controlling devices.

To sense its surrounding environment, the system is equipped with an array of 64 temperature sensors distributed across the surface accessible to bees, therefore enabling the system to capture a detailed thermal snapshot in close proximity to the animals. Auxiliary data regarding hive dynamics and microclimate are obtained using a carbon dioxide sensor and a humidity sensor (Sec. II-B). Additionally, a power sensor measures the input voltage and current drawn by the system, ensuring effective monitoring of the device's performance.

To allow interaction with the animals, the system employs a set of 10 thermal actuators each capable of dissipating 15 W. These actuators are controlled by dedicated digital control loops and driving electronics (Sec. II-C). Additionally, the system is equipped with data storage capabilities via an SD card and supports various communication protocols including USB, CAN, UART, and I₂C. This multi-protocol support ensures that the system can be interfaced with a range of devices such as personal computers, single-board computers, or other microcontrollers located external to the hives.

The USB peripheral serves as the primary method of communication. Its utilization is straightforward, given that the chosen MCU includes the necessary software stack and the physical layer electronics required for establishing communication with compatible devices. Moreover, the robustness of USB is a significant advantage since it employs differential transmission lines and shielded cables, which are highly effective against electrical noise. Also, to guarantee the integrity of the data during transmission, each set of sensory data is accompanied by a checksum. This allows for detection of any data corruption that might occur during transmission events.

To enhance the chances of biocompatibility with bee colonies and with existing hive configurations, the robotic system was designed in the form of a beekeeping frame (Sec. II-D). It consists of acrylic layers encasing a printed circuit board, which serves as the base for the honeycomb and houses all electronic components. Since bees are very protective towards their nest [62], [63], bees and electronics were separated by creating two segregated zones, the “bee arena” where bees can reside and build their honeycombs, and the “electronics bay” where electronic parts are housed inside a protected zone, inaccessible to bees (Fig. 2b).

1) LOW-LEVEL SOFTWARE

The software embedded in the MCU serves as the linchpin for every component of the robotic device. To effectively manage the low-level software execution, we employed a real-time operating system (RTOS, ChibiOS v19.1), chosen for its deterministic behavior. The RTOS's multithreaded scheduler facilitated the compartmentalization of code into three distinct threads: sensing, actuating, and a MicroPython interpreter. Each thread was assured execution within a precise and adjustable time frame. Our inclusion of an

onboard MicroPython interpreter aimed to streamline system parameter adjustments in real-time, eliminating the need to shut down the system, compile, and upload new code after every modification. Additionally, the adoption of a language with simple syntax expanded the system's usability, making it approachable even for individuals without a background in embedded software development.

To increase the reliability and stability of the system during prolonged operation, we implemented the following features. Firstly, we enabled the MCU watchdog timer (IWDG) to reset the MCU upon overflow and prevent system lockups. Each task within the firmware was required to report its execution status. The system handler, upon confirming all executions, would clear the watchdog timer to prevent the microcontroller from resetting. The duration of the IWDG is dictated by the time required to complete the sensing and actuating threads. Secondly, using a combination of the Real-Time Clock (RTC) and hardware registers, to record the reason for resets, allows the system to log and report reset events to the user, further increasing the system's reliability (see also Sec. II-C7).

2) TIMEKEEPING

Accurately timestamping events is important in analyzing bee behaviors over short and long timescales. Therefore, we utilized the microcontroller's Real-Time Clock (RTC) as the reference time source for our system. To enhance time accuracy, the RTC was driven by an external crystal oscillator (ECS ECX-34RR) featuring a temporal drift of 20 ppm, equivalent to ± 1.73 s/day. In order to account for daily time variations, the control device, typically a Raspberry Pi single-board computer, continuously monitored the time offset between the two devices. If this offset exceeded 1 s, the control device issued a command to resynchronize the robotic device's clock.

B. SENSORS

For a robotic system to be able to observe and interact with an animal colony, it must be able to accurately capture the state of the colony. Therefore, a careful selection of sensors must be made to successfully record the dynamics of a colony. Transducers must be sensitive and accurate to the signals of interest, but also small and robust to avoid influencing the animals' behaviors and withstand the harsh conditions of a hive. Moreover, individual sensors may not provide enough information to investigate and interact with collective behaviors. Honeybee groups adapt their behavior to local conditions. As a consequence, bees are rarely static. Therefore, the number of sensors plays a vital role when reconstructing the patterns produced by a group of animals. Finally, sensors must sample the desired variable according to the dynamics of the signals being observed. Here we establish the technical specifications, the constraints arising from the colony and behaviors of interest, and describe the sensor subsystem design and its implementation to fulfill the specifications.

1) TEMPERATURE SENSING

Temperature is a critical variable that demands continuous monitoring within a honeybee colony. It serves as a direct indicator of the overall health status of the colony and plays a vital role in investigating essential social dynamics within it [7], [40], [64], [65]. For example, with the increase in temperature in late winter and during the foraging season, the colony raises new bees (the brood) [54], keeping the temperature of the broodnest tightly regulated between 33–36 °C [19], varying only a few degrees. Conversely, in colder periods, the colony forms a compact cluster to maintain safe temperature levels, known as the winter cluster. Therefore, considering the significance of thermoregulatory collective behaviors for the colony's homeostasis [10], [18], we investigated the thermal sensing requirements for a robotic system to explore a "thermal pathway" for interacting with honeybee colonies.

a: BIOLOGICAL AND ENVIRONMENTAL CONSIDERATIONS

Honeybees have adapted to a wide variety of climates [51], [66]. For colonies found in high-latitude or high-altitude regions, regular winters reach freezing temperatures, while in tropical and arid places, temperatures commonly surpass +40 °C. In fact, bees have been observed living in temperatures of –45 °C [66] and +48 °C [67]. Since colony activities are directly influenced by the ambient temperature [4], [18], a sensor must be able to measure this temperature range.

Thermal dynamics are rather slow within a beehive. During the foraging season, bees heat the broodnest at rates of 0.1–0.2 °C/min [56], [68], while in the winter, bees in the cluster can adapt thermogenesis to rates up to 1.1 °C/min [69]. Therefore, to record the temperature changes of the relevant thermogenic behaviors sensors need a sampling rate of only a few samples per minute. Additionally, the contents of the cells significantly influence the rate at which temperature changes are detected by the sensors. Employing a straightforward model (refer to Supplementary Material, Text S1), we estimate that the time taken by a bee to elevate a cell's temperature by 1 °C ranges from approximately 13 seconds (for empty cells) to 50 seconds (for cells containing pupae).

Furthermore, the atmosphere within a beehive can reach high humidity levels [70], imposing treatments to both sensors and electronic components to ensure their safe and reliable operation in such conditions. Finally, we are interested in interacting with groups of animals engaged in collective behaviors that present some level of motility (*e.g.*, [40], [71]), requiring the system to be equipped with an array of spatially distributed sensors to continuously monitor the signals of interest [72].

b: SENSOR SELECTION

We investigated for sensing solutions that would fulfill the above requirements by having (*i*) a resolution better than

0.01 °C, (ii) low operating current and consequently low self-heating, and (iii) a small footprint, to comfortably fit inside honeycomb cells. In order to minimize part count and consequently the space occupied by the circuit, we focused our survey on silicon-based temperature sensors with on-chip ADC (analog-to-digital converter), which usually also brings the added advantage of reduced noise when compared to analog sensors placed a certain distance from the ADC. After surveying 12 different integrated devices that could meet these specifications (see Table S1 for the list of candidates), we selected the Texas Instruments' TMP117 [73] as the temperature sensor for the robotic frame. This sensor was chosen for its notably small physical dimensions, superior accuracy, and minimal operating current compared to other candidates. Additionally, it was readily available in large quantities from major electronics suppliers.

The TMP117 characteristics (see Table 1) can rival Class AA resistance temperature detectors (RTDs) with a temperature accuracy of ± 0.1 °C over the range -20 °C to 50 °C, and with repeatability of ± 1 LSB (least significant bit). Temperature values are digitized with a 16-bit ADC resulting in a resolution of 0.0078 °C ($= 1$ LSB). In 8-sample averaging mode, the conversion time is 125 ms, equivalent to a maximum sampling frequency of $f_s = 8$ Hz. Moreover, the device has a maximum current demand of $220\text{ }\mu\text{A}$ when in averaging mode, and $3.1\text{ }\mu\text{A}$ when in standby mode (average energy $\bar{E} = V \cdot I_{avg} \cdot t = 3.3\text{ V} \cdot 30.2\text{ }\mu\text{A} \cdot 125\text{ ms} = 12.5\text{ }\mu\text{J}$). The sensor's packaging size of $2\text{ mm} \times 2\text{ mm} \times 0.8\text{ mm}$ can comfortably sit inside the honeycomb cells (Fig. 3a,d).

A positive consequence of the low power required by the sensor is the small self-heating effect that could bias temperature recordings and impact bees. A simplified assessment of the effect of the sensor's dissipated power on temperature readings can be made using the thermal metrics of the sensor packaging and its operating conditions. The package temperature increase can be estimated as $\Delta T = R_{\Theta JT} \cdot P_D$, where $R_{\Theta JT}$ is the junction-to-ambient thermal resistance of the component ($R_{\Theta JT} = 70.7$ °C/W) [73], and P_D is the dissipated power ($= V_s \cdot I_{avg} = 3.3\text{ V} \cdot 30.2\text{ }\mu\text{A} = 99.7\text{ }\mu\text{W}$). For the TMP117 packaging, we estimated a negligible rise of $\Delta T \sim 0.007$ °C. In this estimation, important effects of the PCB structure and environmental factors are not considered but tend to reduce the rise of temperature.

c: SENSOR DENSITY

Some useful information can be extracted from a hive monitored by a small number of sensors [74], [75], [76]. Nonetheless, the dynamic nature of complex collective behaviors typically demands a more extensive sensor array to accurately capture the change of patterns of bees in motion [72]. An insufficient number of sensors could restrict an artificial agent's ability to construct an accurate model of its surroundings, consequently hindering its capability to emit pertinent stimuli for effective interaction with the animals.

TABLE 1. Summary of TMP117 specifications and array configuration.

| Characteristic | Value | Note |
|----------------------------------|--------------------------|----------------|
| Operating range | -20 °C to 50 °C | |
| Accuracy | ± 0.1 °C | |
| Repeatability | ± 1 LSB | |
| Resolution | 0.0078 °C (1 LSB) | 16-bit ADC |
| Conversion time, t_{c_avg} | 125 ms (max. 140 ms) | Averaging mode |
| Conversion time, t_c | 15.5 ms (max. 17.5 ms) | Normal mode |
| Sampling frequency, f_{s_avg} | 8 Hz | Averaging mode |
| Sampling frequency, f_s | 64 Hz | Normal mode |
| Max. current, I_{peak} | $220\text{ }\mu\text{A}$ | Averaging mode |
| Standby current, I_{sby} | $3.1\text{ }\mu\text{A}$ | |
| Packaging Size | $2 \times 2 \times 0.8$ | mm |
| Array size | 64 sensors | |
| Sensor array config. | $5 \times 11 + 9$ HDP | |
| Sensor spacing | H:36.8 mm, V:36.4 mm | |

One of the first systems to use an array of temperature sensors (192 thermocouples)¹ for long-duration monitoring of overwintering colonies was the work developed by C. Owens, in 1971 [71]. It wasn't until the 2000s, almost 30 years past this landmark work, that highly integrated semiconductor devices became easily accessible, allowing a new surge of research using multiple sensors inside hives (e.g., [79], [80], [81], [82], [83]).

In our system, we distributed a regular array of 5×11 sensors across the bee-occupied portion of the frame (the “bee arena”), with horizontal and vertical spacing of 36.8 mm and 36.4 mm respectively (Fig. 3a). This design was informed by several key considerations. We aimed to obtain a high spatial resolution of thermal sensing while also being sensitive to cost, and design feasibility such as routing density and device address space. Since 4×8 TMP117 sensors can be addressed with 8-channel multiplexers, we considered multiples of 32 devices (*i.e.*, up to 32, 64, 96, etc.). Geometric constraints came from the frame's specific aspect ratio and our aim of aligning the sensor placement within honeycomb cells. To avoid disproportionate spacing along the horizontal or vertical axes, we refrained from row/column configurations with a large imbalance. Thus, we opted for an array of 5×11 sensors. Since the address space could accommodate 64 sensors, we also added a high density patch (HDP) of nine sensors, positioned in the central part of the frame, to allow future investigations of high spatial resolution phenomena. In total, the system is comprised of 64 temperature sensors (plus two extra sensors from the CO₂ and humidity sensors located in the electronics bay). To manage the communication with such a large number of sensors, we employed two 8-channel I₂C multiplexers (Texas Instruments TCA9548A) enabling the MCU to continuously scan groups of four TMP117s. After the sensors store the sampled temperature in their internal memory, reading

¹ Precursory works using electronic temperature sensors, albeit applied for short periods of time, were performed by Milner & Demuth, in 1921 [77], and P. Lavie, in 1954 [78], with systems comprised of 14 and 6 thermistors respectively.

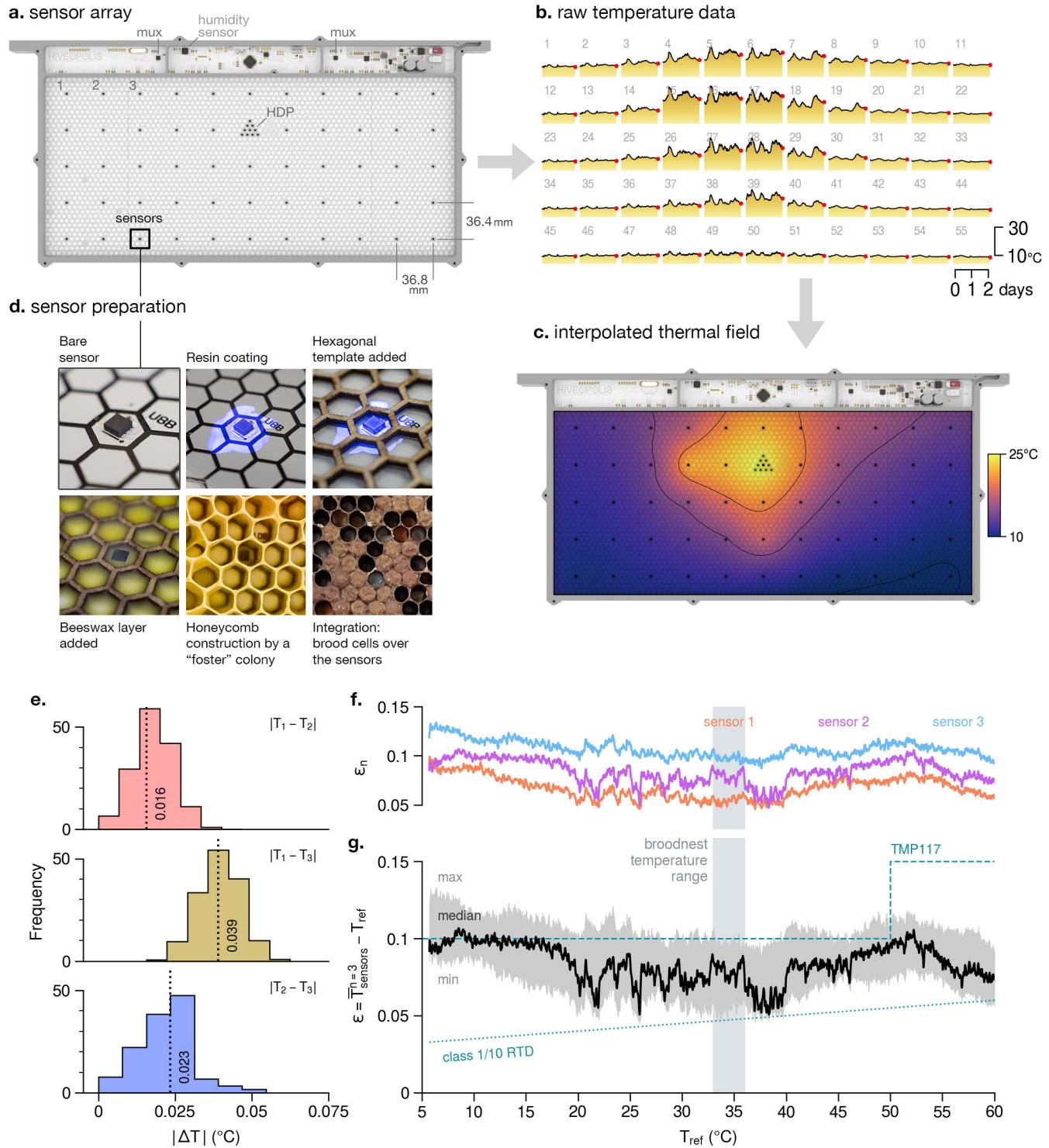


FIGURE 3. Thermal sensing. (a) 3D render showing the temperature sensors' layout and main thermal sensing circuit components on the robotic frame's front face. (b) Raw temperature data graph from the sensor array (excluding nine from the high-density patch) over two November days. (c) Interpolated thermal field on a 3D frame diagram, at 1 mm intervals from 64 sensors. (d) Step-by-step photos of sensor integration into colonies, highlighting resin fluorescence under UV light and a frame patch covered with brood cells. (e) Temperature difference distributions between sensor pairs ranging 6 °C to 60 °C, from a test PCB with three sensors. (f) Differences between each sensor and a calibrated reference thermometer over the experiment's temperature range ($\epsilon = T_{\text{sensor}} - T_{\text{ref}}$), smoothed by a Gaussian filter with $\sigma = 3$. (g) Median uncertainty of three sensors with minimum and maximum values in gray, smoothed by a Gaussian filter. Dashed and dotted blue lines represent the manufacturer's uncertainties for the TMP117 and the calibrated RTD.

all 64 sensors takes approximately 1.5 ms. Example data captured by the sensor array from a colony during winter are visualized to show temporal (Fig. 3b) and spatial (Fig. 3c) patterns. The spatial reconstruction is detailed in Sec. V-C.

d: SENSOR PREPARATION

The temperature sensors are the only electronic components within direct reach of the animals. Therefore, they required safeguarding and adaptation to both minimize interference with the animals and endure the hive's microclimate and any defensive behaviors exhibited by the animals. The following procedures were implemented and validated across 10 robotic units from 2020 to 2023 (see Fig. 3d):

- 1) Each sensor and its metal pads were coated with an acrylic conformal coating (MG Chemicals 419D) to a thickness of 50 μm to 75 μm for moisture protection.
- 2) To constrain access to the sensor pins, and also to induce the construction of wax combs, a hexagonal mesh was fixed to the PCB covering entirely the “bee arena” (see Sec. II-D).
- 3) To assist in the construction of combs, and add an extra protection layer during the process of colonization of the robotic frames, a thin layer of melted beeswax was applied over the “bee arena”.
- 4) At this stage, we introduced the robotic frames into a full-colony box hive, housing up to 40 000 bees, as opposed to the smaller population in an observation hive. This larger number of bees facilitated the comb-building process, as the larger number of individuals meant more resources were available for wax cell construction. Typically, we replaced either one or two of the ten regular frames.
- 5) The duration of comb building varied, typically lasting 2 to 3 weeks, although this period was subject to seasonal variation. Honeybees exhibit different rates of comb construction depending on the time of year, with accelerated activity observed earlier in the season. Once the combs were completed, the robotic frames were transferred to the experimental hives [84].

It is important to note that in preliminary trials, we omitted the use of the hexagonal mesh (*i.e.*, skipped step #2), and covered the robotic device PCBs directly with beeswax. We observed that without the mesh, comb construction was less uniform, had poorer coverage of the device surface or even avoided constructing comb on the PCB surface, and exhibited inferior geometry (*e.g.*, loss of symmetry) compared to frames equipped with the mesh.

e: SENSOR EVALUATION

To test the performance of the TMP117 sensor, we analyzed the data generated by three sensors mounted on a small PCB. We carried out two tests. The first compared the temperature readings from each sensor against each other (Fig. 3e), and the second involved comparing these readings against those from a calibrated reference thermometer (Fig. 3f,g). For both

tests, the PCB, which was covered in a thin polyethylene film, and the reference thermometer were placed in a thermal bath. The bath water was initially cooled to 6 °C with ice, then warmed for 70 min until reaching approximately 60 °C. To ensure a uniform water temperature, a motorized propeller continuously stirred the water. Data samples were gathered every half-second ($n_{samples} = 8363$).

The first test was designed to measure consistency among the three TMP117 sensors. We compared the temperature data recorded by each sensor against each other. By calculating the absolute temperature differences between pairs of sensors, we were able to visually represent value dispersion and estimate any potential bias when all sensors were exposed to the same temperature. Notably, the most significant difference was between sensors 1 and 3, with a deviation of (0.039 ± 0.012) °C, and a maximum deviation of 0.062 °C (Fig. 3e).

The second test was performed to compare the TMP117 sensor values against a high-accuracy temperature probe. For the reference thermometer, we used a calibrated Class 1/10 DIN RTD probe (Process Parameters PPL1-P) connected to an ohmmeter in a 4-wire configuration (HP 34401A) to measure the water temperature. Throughout the experiment, sensor 3 presented the highest maximum offset of 0.14 °C (Fig. 3f), and the median difference between the three TMP117 sensors and the reference thermometer was (0.083 ± 0.014) °C (Fig. 3g).

2) CARBON DIOXIDE AND HUMIDITY SENSING

Humidity and carbon dioxide (CO₂) are critical biophysical parameters in the microclimate inside a beehive [85]. CO₂, a byproduct of bee respiration, serves as an indirect indicator of metabolic activity [86], [87]. High CO₂ concentrations, however, can be toxic to bees, potentially triggering a group ventilation effort known as fanning [57], [85]. Appropriate humidity levels are necessary for healthy brood development, the ripening of nectar into honey, and prevention of water condensation in colder temperatures [66], [70], [88], [89]. Consequently, incorporating sensors for these parameters into the robotic frame could offer valuable data for studying social dynamics.

Considering the constraints of size and the ability to measure high CO₂ concentrations found in bee colonies, not many sensors on the market were suitable. We opted for the Sensirion SCD-30 sensor due to its capability to measure concentrations ranging from 0 to 10 000 ppm, with an accuracy of $\pm(30 \text{ ppm} + 3\%)$ and repeatability of $\pm 10 \text{ ppm}$ [90].

For the humidity sensor, we evaluated a range of commercially available options (Table S2). Two devices emerged as the top contenders, the Texas Instruments HDC2010 and the Sensirion SHT35. While the SHT35 offered slightly better performance with a typical accuracy of 1.5%, compared to 2% of the HDC2010, the latter was more cost-effective and consumed less power, albeit with the slight compromise on

accuracy [91]. Despite these advantages, supply chain disruptions during the COVID-19 outbreak significantly hindered the availability of HDC2010. Consequently, we employed the SHT35 sensor in the device.

C. THERMAL ACTUATORS FOR HONEYBEE INTERACTIONS

In order to interact with animals, a robotic system must be able not only to sense the animal's behavior but also be able to send relevant cues [14]. In a system aimed at studying thermoregulatory behaviors, one way to achieve such interactions is through the use of thermal actuators (TAs) capable of producing cues similar to those naturally experienced by bees. In this section, we describe the design and implementation of such actuators.

1) BIOLOGICAL CONSIDERATIONS

The metabolic heat production of honeybees is subject to significant variation, influenced primarily by ambient temperature and the number of bees engaged in thermogenic activity [18], [87]. Bees generate heat by shivering their wing thoracic muscles, a process that produces heat as a metabolic byproduct [92]. Although an individual bee is capable of generating up to 230 W/kg of heat [18], the thermoregulatory process within a hive is a shared effort. Consequently, each bee's heating contribution is typically less than its maximum capacity. This is particularly evident during winter when the colony collectively regulates the nest's temperature, by transforming the stored honey into heat (chemical energy → thermal energy) and modulating the thermal conductivity of the bee cluster by adjusting inter-bee spacing. Previous research has shown that the collective metabolic rate decreases as the number of bees increases [92], with the colony's peak metabolic rates recorded at 150 W/kg and more commonly around 33.5 W/kg [87]. These values were used to steer the design of the thermal actuators.

To increase the likelihood of bees recognizing the thermal cues emitted by the thermal actuators as originating from their conspecifics (*i.e.*, other honeybees), we strategically integrated these actuators into the comb foundation. Placing actuators within the space that divides the two sides of the robotic device (see Fig. 6a), mirroring the design of beekeeping frames, capitalizes on bees' natural inclination to seek warmth generated by their fellow bees on the reverse side of the frame. Moreover, using an array of multiple actuators within each frame enables localized heat generation in a region where the only natural heat source would be other bees.

2) THERMAL ACTUATORS FROM LONG MEANDED PLANAR TRACES

The robotic system's actuators were devised to be able to dissipate a combined power of 150 W, similar to the peak metabolic activity of a 1-kg colony in winter [87] (this mass equates to ~7700 bees [93]). In order to allow the

TABLE 2. Summary of thermal actuator characteristics.

| Characteristic | Value |
|-------------------------------------|------------------------------|
| Nominal maximum power, P_{act} | 15 W |
| Supply voltage, V_{act} | 12 V |
| Nominal resistance, R_{act} | 9.1 Ω |
| Measured resistance, \bar{R}_{TA} | (7.85 ± 0.63) Ω |
| Current at P_{max} , I_{act} | 1.3 A (= V_{act}/R_{act}) |
| Trace material | Annealed copper |
| Trace height, h_t | 35 μm (1-oz. copper) |
| Trace width, w_t | 0.267 mm |
| Total trace length, ℓ_t | 4852 mm |
| Geometry | Square with 74.7 mm sides |
| Total number of actuators, n_{TA} | 10 (= 5 × 2 array) |

production of thermal cues with distinct spatial patterns, we distributed ten actuators into a 5 × 2 array (Fig. 4a-c). Current flowing through a resistor will dissipate some energy in the form of heat - Joule heating (electrical energy → thermal energy). Following this principle, for each thermal actuator, we designed a conductor with a specific value of resistance able to dissipate a maximum of $P_{act} = 15$ W. For a system powered by a 12 V supply, each thermal actuator must have a maximum resistance of $R_{act} = V_{act}^2/P_D = 9.6$ Ω. We opted to use a $R_{act} = 9.1$ Ω to allow an extra power dissipation margin ($P_D = 15.8$ W) and the availability of commercial resistors with this nominal value, in the E24 series, simplifying the evaluation and testing of the driving circuit.

With a printed circuit board (PCB) used as the central foundation of the system (Sec. II-D), we utilized one of the outermost copper layers to design the planar actuators. The necessary trace length to achieve the required resistance was found via $\ell_t = (R_{act} \cdot w_t \cdot h_t)/(\rho_{cu} \cdot [1 + \alpha_{cu}(T - T_0)])$, where w_t and h_t are the width and height of the trace, ρ_{cu} is the copper resistivity, and α_{cu} is the copper resistivity thermal coefficient. For a trace width of $w_t = 0.267$ mm and height $h_t = 35$ μm (copper weight of 1-oz.) we calculated a trace length of $\ell_t = 4852$ mm. With the objective of achieving a higher temperature homogeneity, we chose to design the heater pattern based on a Hilbert space-filling curve [94]. A Hilbert fractal can be created by the iteration of replicas of a rotatable seed geometry. This process is illustrated in Fig. 4d, showing the initial iterations, $n = 1$ to 3, and the final heater pattern generated by a 6th order Hilbert curve. To create a space-filling curve with the required length ($\ell_t = 4852$ mm), each segment of the curve should be $\ell_t/(4^{order} - 1) = 1.185$ mm long, resulting in a final actuator with a square geometry having 74.7 mm sides. These specifications and results are summarized in Table 2.

3) DRIVING CIRCUIT

To regulate the power delivered to each thermal actuator, each of the ten drivers is controlled by a pulse-width modulated (PWM) signal originating at the MCU (Fig. 2a). The activation duration (*i.e.*, period when current is flowing through

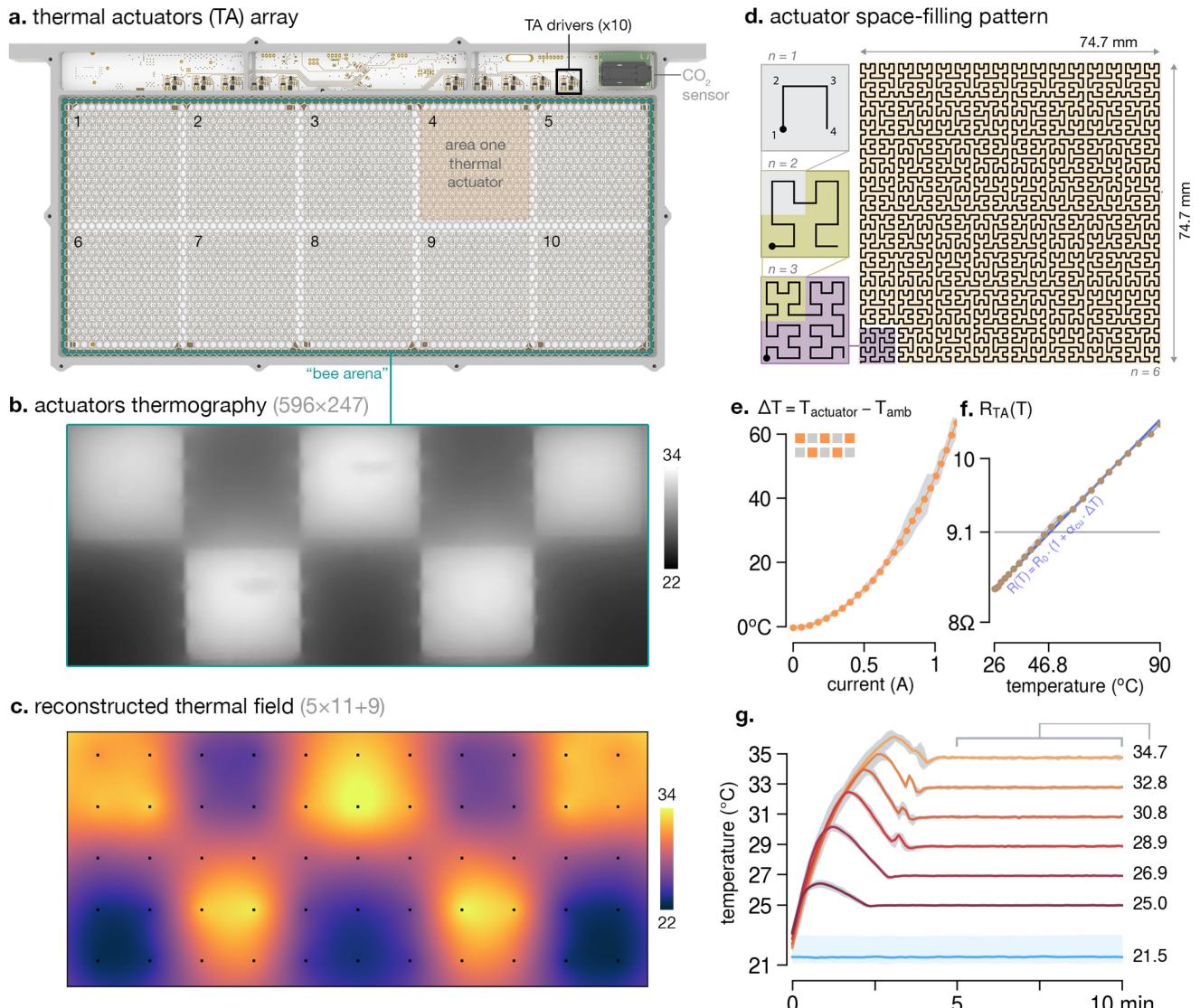


FIGURE 4. Thermal actuator design and characterization. (a) 3D rendering of the robotic frame’s backside showcases the placement of the ten thermal actuators (TA) and their driving circuits. (b) Thermography of the “bee arena” (FLIR T650sc, $\epsilon = 0.95$), demonstrating the system’s ability to generate complex thermal fields, with image cropped to 596 × 247 px showing only the “bee arena”. (c) System’s thermal field reconstruction using 64 temperature sensors, mirroring features shown in the high-resolution thermography. (d) Final metallic pattern of the thermal actuator based on a 6th order Hilbert curve. (e) Median temperature rise at the actuators’ center against current input, with the orange curve for five actuators and the gray curve showing combined uncertainty (MAD plus instrument error). (f) Resistance variation of TAs with temperature change. Target resistance of 9.1 Ω met at 46.8 °C. The blue line reflects the theoretical copper resistance change ($\alpha_{cu} = 0.003\ 95\ ^\circ\text{C}^{-1}$). (g) Median temperature profiles for 10 actuators across six target temperatures, with gray curves for MAD and right-side values showing median temperatures in the final 5 minutes. The blue area indicates the lab temperature range during experiments.

the TA) is adjusted by each of the numerical controllers running in the MCU and reflected in the changes to the duty cycle of the control signal. This PWM signal is injected into a gate driver chip (Texas Instruments UCC27517A) that can rapidly turn on or off an N-channel power MOSFET transistor (Vishay SiSS12DN). To minimize heat dissipation by the transistor, the selected part has a low “on” resistance, typically lower than $R_{on} \leq 3\ \text{m}\Omega$. We also added flywheel diodes to protect the actuators’ driving circuits from voltage spikes produced by stray inductance when the TAs are turned off.

4) THERMAL PROFILE OF TAS

To establish the temperature profile of the thermal actuators, we applied a constant voltage for a period of 10 minutes when measuring the temperature at the center of the actuator. We used an RTD rated 100 Ω at 0 °C (Thorlabs TH100PT, $u_{pt100} \pm 0.3 + 0.005 \cdot |T|^\circ\text{C}$, where T is temperature) connected to a digital multimeter in a Kelvin (four-wire) configuration (HP34401A, $u_{res} \pm 51\ \text{m}\Omega$). The electrical current flowing through the actuator was also recorded using the power supply data interface (Rigol DP832A, voltage and current uncertainties of 0.05% + 10 mV and

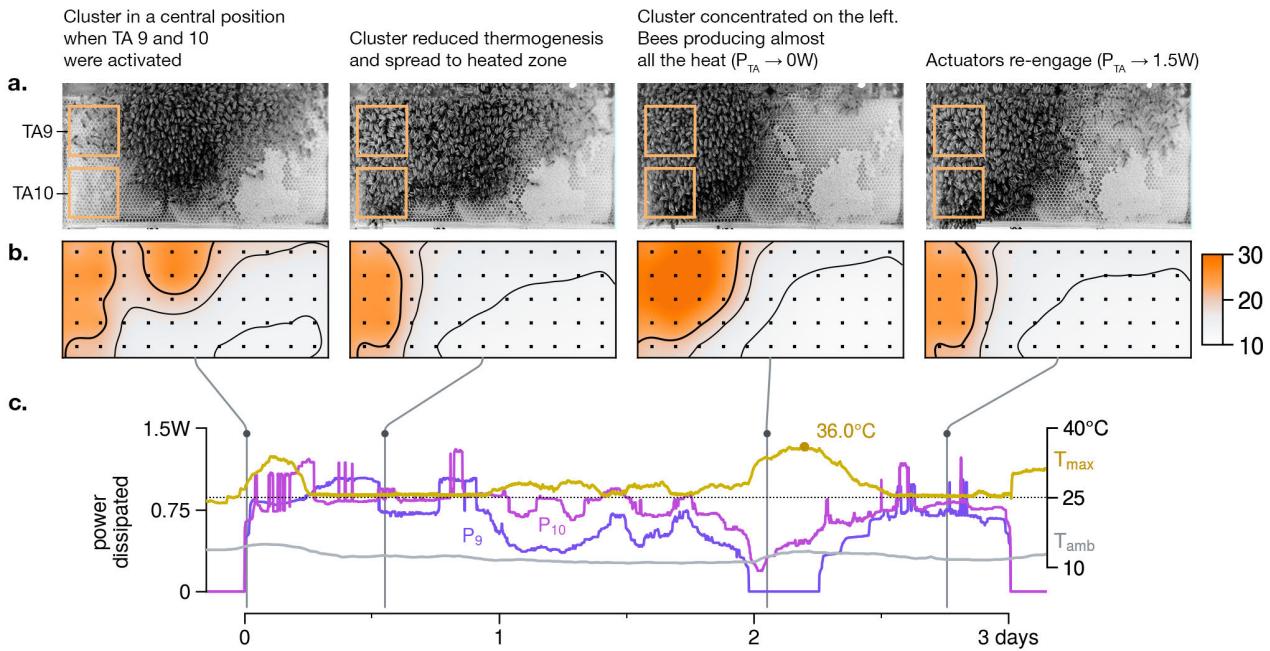


FIGURE 5. Bioacceptance of the thermal actuators. (a) The activation of two thermal actuators (orange rectangles) at 25 °C lured bees. The “free energy” provided by the robotic system attracted a winter cluster comprised of approximately 4000 bees. (b) Initially, the thermal fields of actuators and bees are distinguishable. After approximately 12 h the fields merged. The thicker black line represents the 22 °C isotherm. (c) Since we adopted an animal-in-the-loop strategy, at moments bees “allowed” the robotic system to engage more (for example at $t = 0.5$ days) or less ($t = 2.25$ days). The dissipated power by the two active actuators is depicted by the purple lines, and the maximum temperature on the frame surface T_{max} by the yellow curve. Data smoothed via a median filter with a 2-h kernel.

0.15% + 5 mA). To establish the temperature variation for a specific supplied voltage, we calculated the median temperature of the last 10 seconds ($n_{samples} = 10$) when the temperature had stabilized (not changing more than 0.4 °C in the last minute), and subtracted from it the ambient temperature value ($\Delta T = T_{actuator} - T_{amb}$). The ambient temperature in the lab, T_{amb} , was recorded as the median value of 64 temperature sensors from an additional robotic system installed adjacent to the experiment ($d \sim 1$ m). This procedure was performed for voltage steps of 0.25 V between 0 V to 12 V, and repeated on five thermal actuators. Increasing the applied voltage, and therefore the supplied current ($I = V/R$), we observed similar behavior in all tested actuators, displaying an exponential temperature increase (Fig. 4e).

5) ELECTRICAL CHARACTERIZATION OF TAS

In order to quantify the deviation of the manufactured actuators’ resistance R_{TA} from the nominal (designed) value of $R_{act} = 9.1 \Omega$, we measured the resistance of 110 thermal actuators, from 11 PCBs, using the same 4-wire configuration described above. The measured resistance of the TAs was $\bar{R}_{TA} = (7.85 \pm 0.63) \Omega$ ($n_{TA} = 110$, $\bar{T}_{amb} \sim 23$ °C), a difference of -1.25Ω to the target value. It is important to note the inevitable resistance drift due to the non-negligible copper resistivity thermal coefficient, which precludes the possibility of precisely defining the resistance value for the thermal actuators (Fig. 4f).

Despite the difficulty in fixating thermal actuators’ resistance, the closed-loop controller automatically compensates for these resistance fluctuations by adjusting the flow of current (and therefore the dissipated power), thereby ensuring that the target temperatures are consistently maintained.

6) CONTROLLERS

We devised two methods to control the power delivered to thermal actuators. The first method, a simple constant power controller, allows users and programs to directly adjust the duty cycle of the PWM pulse that rapidly activates and deactivates the actuators. The second method uses a numerically implemented PID control loop to adjust the actuator temperature, with feedback from the temperature sensor array. Although variability in resistance due to manufacturing (Sec. II-C5) or due to variations from temperature (Fig. 4f) would influence the power dissipated by the direct PWM adjustment method, the PID control loop that adjusts the duty cycle according to temperature feedback is not sensitive to such variability. Each thermal actuator has a controller that is influenced only by the sensors mounted directly on top of the actuator. The ten control loops are executed in a dedicated thread of the RTOS (Sec. II-A), immediately after the execution of the sensor thread, and updated at intervals of 10 s. We performed an experiment to quantify the thermal regulation capabilities of controllers and thermal actuators together. Using an empty robotic frame installed vertically in an observation hive, we activated each of the

ten actuators for a duration of 10 min with six different objective objective temperatures T_{obj} , from 25 °C to 35 °C (Fig. 4g). In the experiment, it took a bit less than 4 min for temperatures to stabilize. The highest overshoot occurred at a target temperature of 29 °C, reaching a median overshoot of 3.5 °C ($n = 10$). Once the controller reached a steady state, the highest offset between setpoints and the median temperature of the last 5 min was -0.29 °C, at $T_{obj} = 35$ °C. The maximum deviation between two sensors across the actuator surface (*i.e.*, thermal inhomogeneity) had a median value of (2.66 ± 1.89) °C. During the experiment, the lab temperature was $\bar{T}_{amb} = (21.5 \pm 0.4)$ °C.

To improve the bio-integration of the system and increase the odds of acceptance by the colony, we fixed the frequency of the ten PWM channels to 5 kHz. This value is above the bee's spectral response to sound and vibration [95], therefore minimizing the chances of spurious vibrations that can disturb honeybee behaviors such as the waggle dance [96]. Furthermore, the default limit to the rate of temperature change is adjusted to 2 °C over 10 min, a value observed in larval cells [56].

In our final effort to enhance the bio-acceptance of the thermal actuators, we implemented an “animal-in-the-loop” configuration [60], wherein the same sensors measuring thermal behavior also provide temperature feedback to the controllers. To assess the actuators' influence on honeybees, we activated the two leftmost actuators at time $t = 0$, setting them to a target temperature $T_{obj} = 25$ °C. This was done when a winter cluster was positioned near the center of the robotic frame (refer to Fig. 5a,b, illustrating the thermal patterns from both actuators and bees). The actuators' maximum combined power was limited to 3 W. However, during the three-day experiment, they operated at less than half their maximum capacity, averaging $44\% = (1.32 \pm 0.44)$ W (median \pm MAD). For the initial 1.75 days, we observed a combined heating effort from both the bees and the robotic device, indicated by T_{max} consistently nearing the set target ($T_{obj} = 25$ °C, as seen in Fig. 5c). Around day 1.75, despite no significant change in the ambient temperature [$T_{amb}(1.75) = 10.9$ °C], the bees began to increase the cluster temperature, reaching a peak at $T_{max} = 36.0$ °C, ($T_{amb} = 13.3$ °C). This caused the actuators to disengage. After a period of reduced activity, the actuators re-engaged, as indicated by the rise in dissipated power (purple curves at $t = 2$ days in Fig. 5c). Due to the short duration of this experiment, it was not possible to conclude whether there was a time dependency on the animals' response, like habituation (see Sec. III-B for a longer-term experiment). This brief experiment confirmed the actuators' operational efficacy in the presence of animals.

7) SAFETY MECHANISMS

Our previous measurements present evidence that the thermal actuators are capable of reaching dangerous temperatures, enough to melt wax and harm animals (Fig. 4f). For

this reason, many safety mechanisms were implemented in the hardware and at the low-level firmware. During the validation phase of the system, a 3A resettable fuse was installed upstream of the actuators' power supply, limiting the maximum power dissipation to 36 W. Another protection feature was implemented in the PID controllers, where the total current drain is limited, by default, to 1 A. Furthermore, the controllers were programmed to disable the actuators if sensors stop responding or if the controllers do not respond for more than two minutes. Finally, two temperature thresholds are in place. A soft and adjustable limit is initially configured to 35 °C, and a hard-coded limit is at 47 °C.

D. MECHANICAL CONSTRUCTION AND FORMING A BIOHYBRID SOCIETY

The mechanical design of the robotic beekeeping frame revolves around its acceptance within a bee colony, not by mimicking bees' appearance but through the integration of shapes and materials already successful in agricultural beekeeping. The robotic frame takes on the dimensions of a standard Zander beekeeping frame, measuring 420 mm × 220 mm, ensuring compatibility with widely used agricultural and observation hives. The frame structure was constructed from six laser-cut layers of acrylic with the PCB in the center serving as a foundation for the combs (Fig. 6a). Modern materials like plastics have long been incorporated into honeybee colonies [97]. We opted to use PMMA (polymethyl methacrylate), also known as acrylic or plexiglass, a thermoplastic frequently employed in various engineering applications due to its mechanical properties, such as ease of machining. The decision to use it as the material for the frame structure was also influenced by its biocompatibility. Acrylic has been used extensively in beehive construction and bee-related research for several decades (*e.g.*, [98], [99], [100]). Adjoining the PCB are layers of 1-mm thick wood (or optionally acrylic), which are cut into a hexagonal pattern to guide bees in their honeycomb construction activities [101] (see Fig. 3d). The hexagonal cells were designed to have inner minor and major axes of 4.55 mm and 5.25 mm, and wall thickness of 0.7 mm. To bolster structural rigidity and to demarcate an electronics bay isolated from the bees, two additional acrylic layers were integrated into the design (Fig. 6a, blue and green structures). All cut parts were rinsed with isopropyl alcohol to remove small debris and eliminate any residual odors from the laser-cutting process. Once assembled, the region occupied by bees, the “bee arena”, has a surface area of 410 mm × 180 mm per side (Fig. 2b). The entire assembly is held securely using 2-mm nylon screws.

Having the PCB as the foundation for the honeycombs was important since its epoxy-fiberglass substrate has a thermal conductivity similar to beeswax, at approximately $\kappa \sim 0.3$ W/m°C [102], [103].

To protect the electronics from the high-humidity atmosphere of a hive [70], all electronic components received a

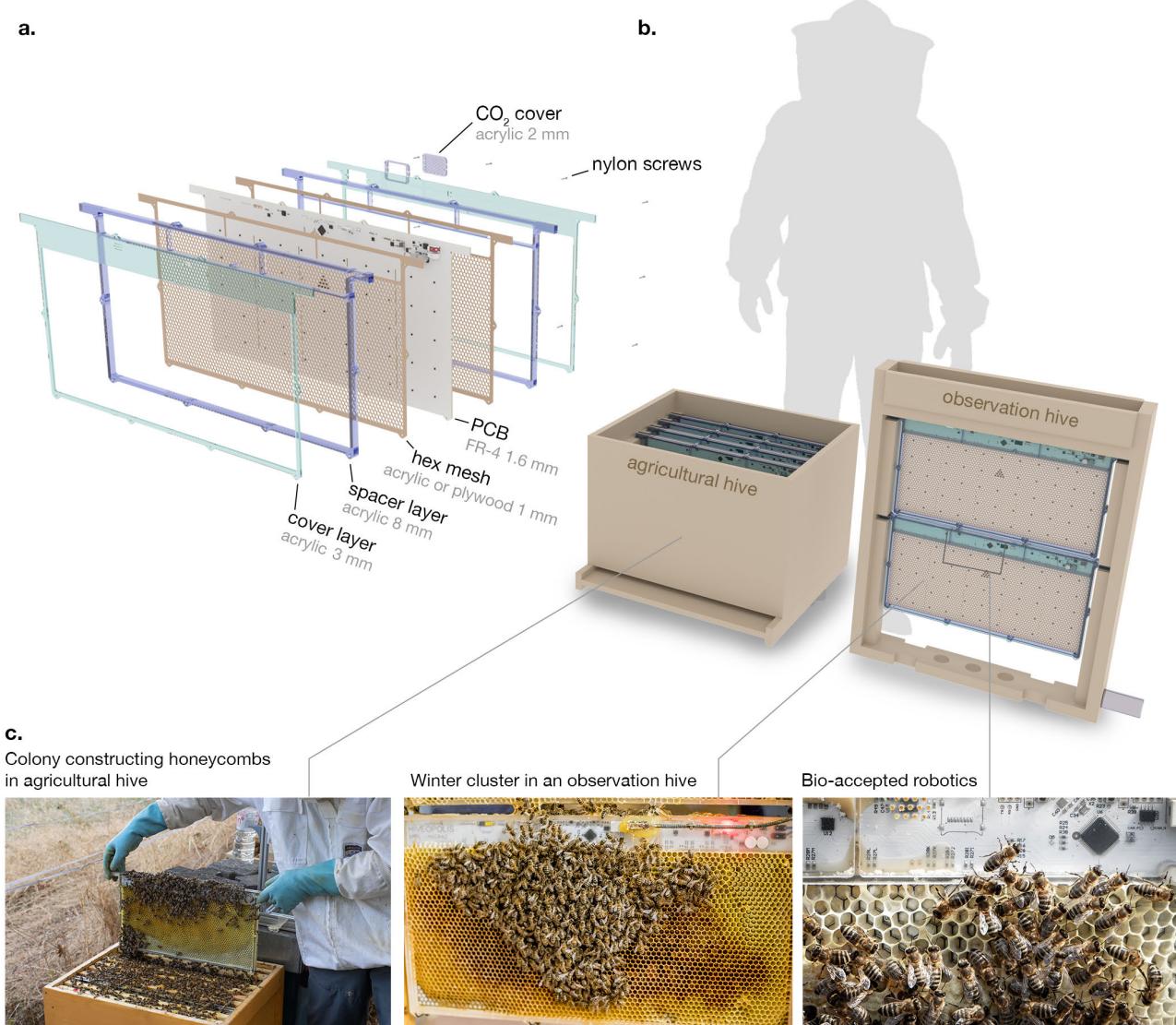


FIGURE 6. Mechanical design and bio-acceptance. (a) An exploded view of the robotic beekeeping frame parts and its materials. (b) Hive types: illustration of the robotic devices installed into box and observation hives. (c) Photos of the device installed into hives and accepted by the colony.

layer of the same protective resin used in the temperature sensors (see Sec. II-B1, Sensor preparation). Prior to the frame’s introduction into a hive cables for power and data were affixed securely to the frame structure.

Before initiating experiments, frames were “incubated” in a large foster colony within box hives to accelerate the comb construction (Fig. 6c). Typically, bees took two to three weeks to build over the hexagonal mesh on both sides of the device. Once the frames were sufficiently constructed, they were moved to the experimental hives and populated with a suitably sized colony. Often, we utilized part of the foster colony to populate these experimental hives and introduced a new queen.

III. A BIOHYBRID SOCIETY TO STUDY HONEYBEES

The successful establishment of a biohybrid society hinges on the effective observation and modulation capabilities of

the robotic elements. One of the robotic system’s primary objectives is to facilitate the comprehensive observation of group dynamics (*i.e.*, “reality mining” [15]), enabling in-depth examination of significant portions of the colony at a high sampling rate. Furthermore, a pivotal facet of designing such a mixed society lies in establishing an efficient communication channel between artificial and living agents [14] allowing the interaction between the two. To evaluate the system for these crucial capacities, we performed two experiments: a long-term observation of a colony and a perturbation experiment aimed at modulating the collective position of a winter cluster, an aggregation behavior initiated when temperatures are low.

A. OBSERVING COLONY LEVEL DYNAMICS

To assess the performance of our system in observing colony-level thermoregulatory behaviors (Sec. II-B), we

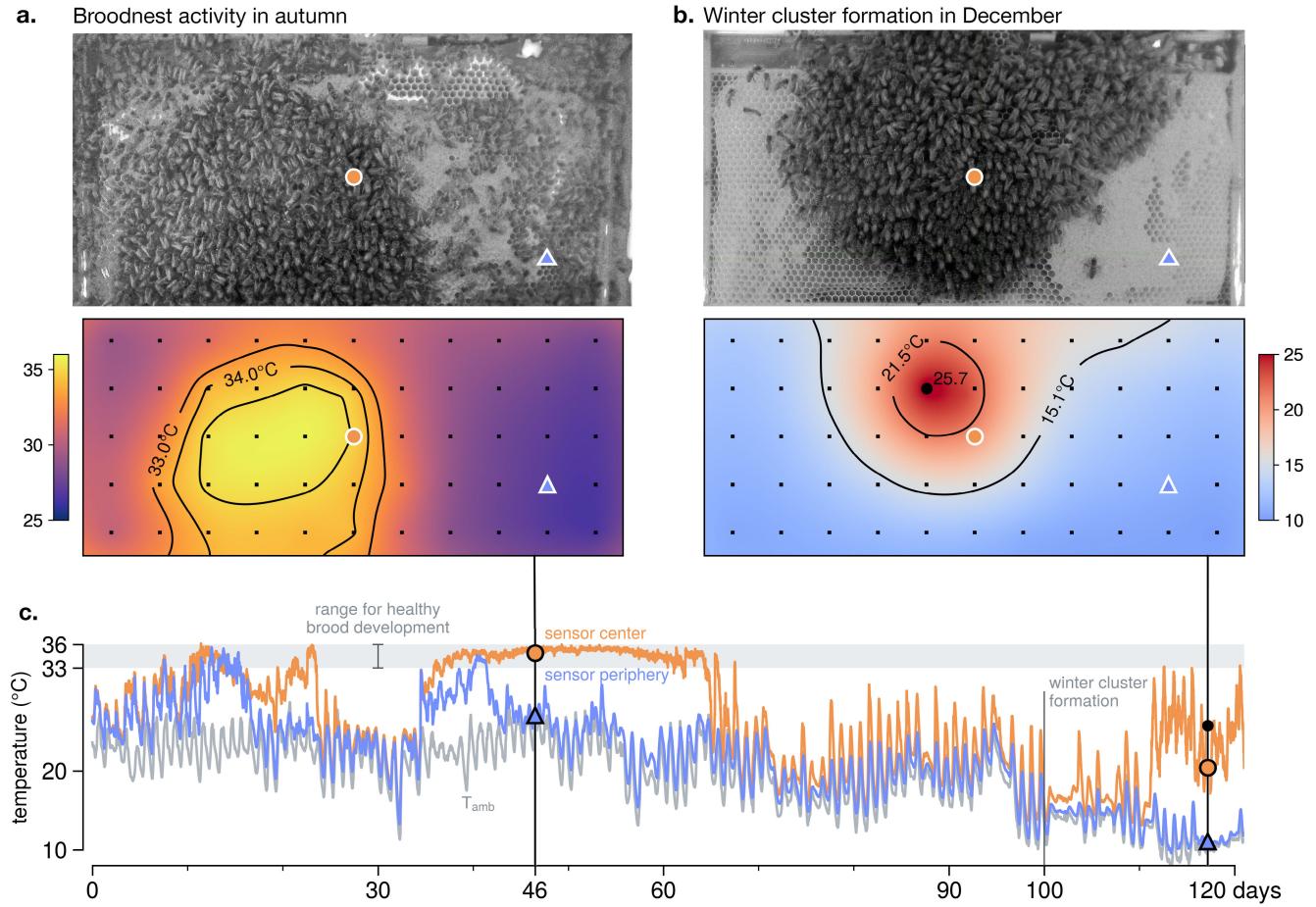


FIGURE 7. Long-term observation reveals thermoregulatory collective behaviors. (a) A photograph and thermal image of a robotic frame during the foraging season, showing nursing bees around capped cells, indicating brood presence. (b) Photograph and thermal image in colder conditions (ambient temperatures around $T_{amb} = 10^{\circ}\text{C}$), with isotherms outlining the cluster’s core ($T_{core} = 21.5^{\circ}\text{C}$) and mantle ($T_{mantle} = 15.1^{\circ}\text{C}$) [40]. (c) Time series of temperatures from two sensors: one centrally located in the ‘bee arena’ (orange), and the other at the frame’s periphery (blue), alongside with T_{amb} .

introduced a robotic frame into an observation hive housing a colony of approximately 4000 bees (see Sec. V-A). We present data spanning 121 days, which encompassed two critical periods within a honeybee colony’s life cycle: the foraging season and the cold season.

During the warmer months, foraging bees venture out of the hive to gather essential supplies such as nectar, pollen, and water. Inside the hive, groups of young worker bees perform a decentralized collective thermoregulation of the broodnest. As discussed earlier (see Sec. I-C), nursing bees regulate the incubation temperature within a thermal range for healthy brood development, from 33°C to 36°C [4]. These temperature values are maintained throughout at least one brood cycle, spanning from the queen laying the egg until the emergence of an adult bee, which typically lasts around 21 days for worker bees. In Figure 7, we show that the distinguishing spatial and temporal characteristics of the broodnest [79] could be observed by the robotic frame. For example, on day 46 of the experiment, the measured thermal field displayed a well-defined heated area (Fig. 7a) kept within the temperature range of 33°C to 36°C (gray horizontal band in Fig. 7c), characteristic of the

broodnest [104], and covering approximately $A_{33^{\circ}\text{C}} = 31\%$ of the “bee arena” (Fig. 7a). Inspecting the data produced by one sensor located inside the broodnest region (data → orange curve, and sensor → orange circle), we observe that the temperature regulation persisted for a duration of 23 days, which encompasses a brood cycle. Furthermore, the presence of brood cells could be verified by inspection of the hive and via photographic evidence.

Around day 100 of the experiment, when the ambient temperature dropped below 15°C , we observed the colony clustering and forming the characteristic ellipsoidal shape of a winter cluster [71]. An example of this collective effort to maintain safe temperatures is shown in the thermal field from day 117 (Fig. 7b), with the highest temperature at the center of the cluster at 25.7°C (Fig. 7b,c ●), a difference of $+15.6^{\circ}\text{C}$ in relation to the surrounding temperatures, T_{amb} .

B. MODULATING COLLECTIVE BEHAVIORS

In a second experiment, we investigated whether the artificial cues generated by groups of thermal actuators (Sec. II-C) could influence the position of a winter cluster comprised of 1200 bees (Sec. V-A). In an observation hive with two robotic

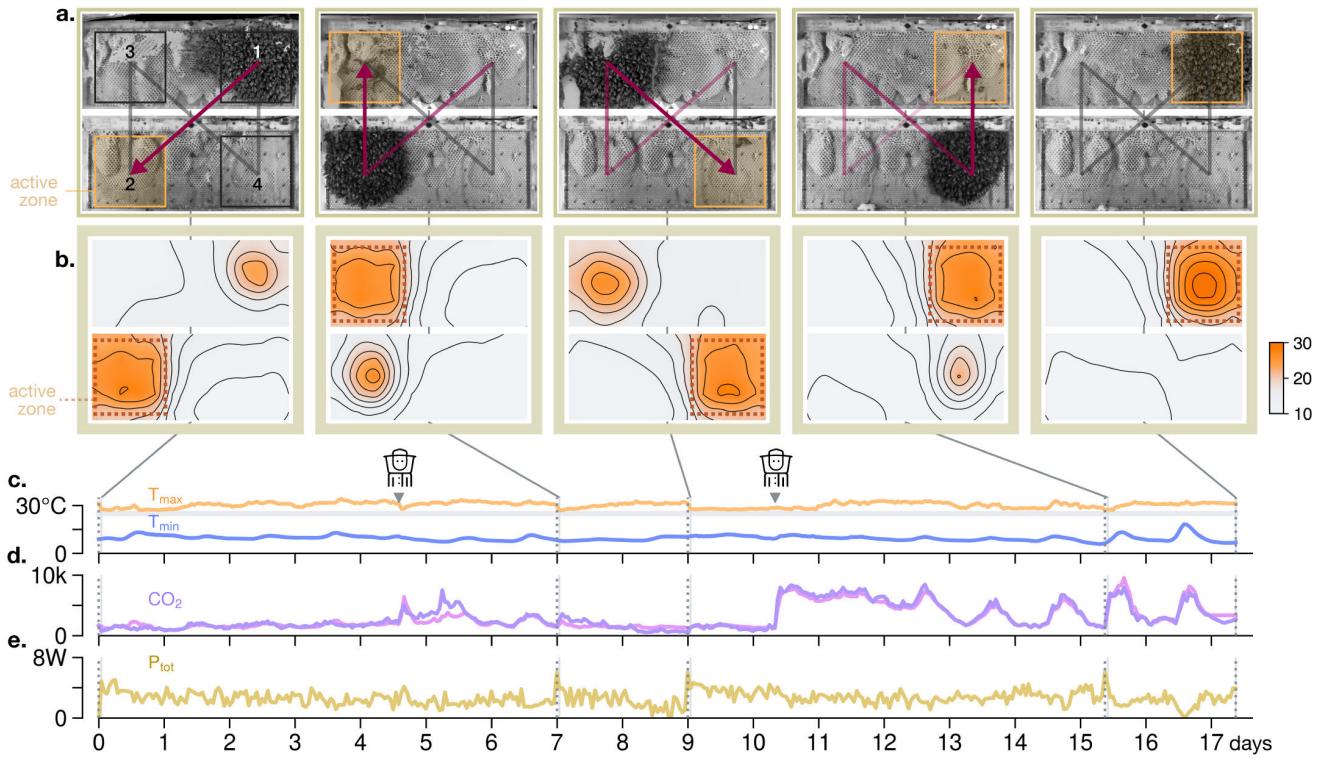


FIGURE 8. Robot modulated honeybee collective dynamics. (a) Photos of the colony in a double-frame observation hive one hour after the transition to a newly activated zone, with arrows showing the sequence of actuator activation (current active phase in red) and thermally active zones in orange rectangles. (b) Corresponding thermal fields with isotherm lines at 2.5 °C intervals. (c) Time series depicting the hive's maximum temperature (T_{max}) in orange, minimum temperature (T_{min}) in blue, with the thermal actuators' set point (T_{obj}) shown as a gray horizontal line. Gray dotted vertical lines mark new zone activations, and beekeeper icons denote colony inspections and feedings. (d) Carbon dioxide levels from the top and bottom frames, in purple and pink, respectively. (e) Total power dissipated by active thermal actuators, showcasing data from the second 17-day iteration cycle with $T_{obj} = 25$ °C. For data from the first cycle ($T_{obj} = 30$ °C), refer to Supplementary Material Fig. S1.

frames, with a total surface of 2952 cm² (= 2 frames × 2 sides × 410 mm × 180 mm), we sequentially engaged one set of actuators to try to attract bees to one of the four predefined zones, as illustrated in Figure 8a. Once the majority of the cluster had congregated in the designated area, we manually triggered the next zone. The activation sequence was intentionally defined to form an unusual \bowtie -shaped pattern and included the activation of “distant” actuators, thus producing non-contiguous heated zones that required the bees to traverse unheated spaces.

The \bowtie -loop trajectory was performed twice. In the first loop, the four thermal actuators of each target zone were activated to 30 °C (Fig. S1), and in the second loop TAs were activated to 25 °C (Fig. 8). In both cases, the bees followed the unnatural trajectory that the robotic system presented, taking approximately 35 days for the two trajectories. During the experiment, the ambient temperature remained between 3.8 °C to 15.5 °C.

The bees consistently maintained the cluster’s core temperature slightly above that of the actuated zone, as illustrated in Fig. 8c. During the initial 17 days of the \bowtie -circuit, the cluster exhibited an average maximum temperature of $T_{max} = (35.0 \pm 1.1)$ °C. Conversely, in the second circuit with the actuators set to 25 °C, the average maximum

TABLE 3. Duration of transitions in the modulation experiment.

| movement | $T_{obj} = 30$ °C | | | $T_{obj} = 25$ °C | | | | | $duration$ |
|----------|-------------------|---|---|-------------------|---|---|-----|---|------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| Diagonal | 12 | — | 3 | — | 7 | — | 6.4 | — | 7.1 days |
| Vertical | — | 2 | — | 1 | — | 2 | — | 2 | 1.75 days |

Cells shaded in light gray are relative to the period shown in Fig. 8, and in darker gray to Fig. S1.

temperature reduced to $\bar{T}_{max} = (30.9 \pm 1.7)$ °C. Notably, in both instances, the maximum temperature was consistently around 5 °C higher than the targets set for the actuators ($T_{max} \sim T_{obj} + 5$ °C).

During the eight transitions necessary to complete the \bowtie -trajectory twice, the cluster took on average 4.1 times longer to perform a diagonal “jump” compared to vertical movements (as summarized in Table 3). This difference is likely due to the longer distances covered by the diagonal path and the presence of a colder region between the cluster and the newly activated region. Furthermore, when analyzing the cluster’s response times to similar movement types (only vertical or diagonal subsets), we found no notable variations in response.

Interestingly, during the modulation experiment, the bees consistently maintained the hive's maximum temperature T_{max} at approximately 5 °C above the actuator's target temperature, T_{obj} . The reasons for this offset warrant further investigation. Carbon dioxide measurements from both frames revealed similar concentration levels (Fig. 8d), suggesting that a single CO₂ sensor might suffice for studying hives of comparable sizes.

Together, these findings demonstrate the capacity of robotic systems to actively shape and direct collective behaviors within a honeybee winter cluster using thermal cues. This highlights the effectiveness of the thermal pathway as a means for fostering interactions between machines and complete honeybee colonies.

IV. DISCUSSION

In this work, we detailed a robotic platform with results evidencing the formation of a biohybrid society comprising a honeybee colony and an autonomous robotic honeycomb. This is a noteworthy advance, addressing challenges in studying the collective behaviors of groups of thousands of individuals sensitive to their social and physical environments [13], [15], [105]. We provided technical details about the robotic device design, considering biological and scientific requirements (Sec. II). We characterized the sensing and actuation capabilities of the device in the lab. The performance evaluation of the robotic system with honeybees involved two separate colonies. In one experiment, a robotic device monitored collective thermoregulatory behaviors for 4 months and was able to observe vital group dynamics during both warm and cold seasons (Sec. III-A). In a second experiment, the collaboration between two robotic devices influenced the movement of a large number of bees along a \bowtie -trajectory, displaying the devices' ability to modulate colony-level collective dynamics (Sec. III-B).

The thermal dynamics of the honeybee hive are one of the most informative quantities about the colony [18]. Some foundational works investigated the spatiotemporal distribution of thermal fields of winter clusters [71] and brood nests [79]. This topic remains relevant and continues to attract new research and the development of instruments to observe the spatial distribution of in-hive thermal fields (e.g., [81], [82]). During the observation experiment, which spanned 121 days, the robotic device provided a continuous view of the hive's thermoregulatory behaviors across different seasons with high spatiotemporal resolution. This long-term observation allowed us to identify critical group dynamics that are evident during the brood-rearing period and in winter when the bees form a winter cluster (Sec. III-A).

In the collective modulation experiment, the system adeptly guided the winter cluster's movement along an unconventional trajectory between two robotic frames (Sec. III-B). Over 35 days, the two devices influenced the displacement of the winter cluster, demonstrating the

effectiveness of the actuator across different target temperatures (T_{obj}). Inspecting the transition times to newly activated regions (see Table 3), we infer that this specific colony did not habituate to the thermal cues during the 35-day period. This finding is consistent with results reported in [40], where another colony exhibited a sustained response to repeated thermal cues from a single robotic frame presented over 51 days. Here we extended the evidence that bee clusters can traverse colder regions to access distant warm spots, challenging existing theoretical models of cluster formation and self-organization as discussed in [40].

Despite the growing interest in using robotics to investigate biological systems, only a few studies have successfully integrated robotic devices into honeybee groups (e.g., [22], [38], [41], [42], [106]). The robotic device in the present paper offers two relevant advances. Firstly, it tightly integrates the “scientific instrument” into the research subject, enabling scientists to monitor the colony from within (Fig. 1, Fig. 3d, Fig. 6c). Secondly, it showcases the ability to interact with entire honeybee colonies as they forage in their natural environment. These two advances are significant because they simultaneously enable (a) detailed investigation into honeybee thermal dynamics (b) within a complete social and environmental context. Specifically, the ability to automate the generation of arbitrary thermal stimuli at different locations within the colony facilitates experiments to investigate, for example, thermal preferenda [107], the effect of heating throughout winter on colony state [71], [108], or responses to localized thermal stress [104], as well as the injection of thermal stimuli that adapt to the animal behaviors. Moreover, works investigating hive temperatures have depicted recordings over long periods but with small sensor count [72] or detailed spatial recordings but for short periods [64], [79]. In contrast, the results above illustrate temperature recordings with high resolution in spatial and temporal dimensions that enable the tracking of collective thermal behaviors.

Although the robotic system showcased promising results, certain limitations were observed. For instance, although the steady-state average temperature of the actuators was precisely regulated (Fig. 4g), there were observed differences of up to 2.7 °C in the uniformity of the thermal field across the actuator surface, as discussed in Sec. II-C. Such variations are particularly critical in studies that require precise thermal uniformity, highlighting an area in need of improvement. To address this, future modifications could include reducing the size of the actuators, altering the PCB design and its layer stack-up to minimize the number and size of copper structures (such as traces and planes) beneath each actuator, and introducing horizontal slots between the rows of top and bottom actuators to enhance thermal isolation.

Furthermore, with the promising results of the robotic device thus far, we can envision integrating additional sensor modalities to broaden the system's observation capabilities. For instance, sound sensors have been effectively used to identify the presence of the queen [109] and to detect

swarming behaviors in the colony [110]. Another intriguing further development could involve employing specialized gas sensors, which may facilitate the detection of *Varroa destructor* mite infestations within colonies [111]. Also, expanding the number of thermal actuators by reducing their size would enhance the device's stimulation capacity and directly improve its interaction abilities. Finally, expanding the current hardware capabilities to enable wireless data transfer would eliminate the need for one cable and enhance the system's overall robustness.

As we intensify the use of the robotic platform and start delving deeper into studying bee colonies, some intriguing questions arise. For example, to what extent do the bees interpret the signals from the thermal actuators as social cues as if from their peers (see [12]), as opposed to merely environmental changes within the nest? When actuators replay temperature time series recorded from winter clusters, are they more attractive to the bees in comparison to fixed setpoints (see [29])? Here, it is worth noting that besides synthetic thermal patterns and replaying natural trajectories, our system could also over-express stimulus trajectories – akin to robotic models over-expressing morphological features [46] or behavioral ones [112]. Experiments aiming to identify robot-mediated thermal profiles that stimulate a small colony to behave similarly to a larger non-stimulated colony may provide insights into these questions of ‘social integration’ of the robots [12]. How do varying internal and external environmental conditions impact the capacity of these thermal actuators to influence behaviors? Using our robotic systems to modify hive-internal conditions, in conjunction with a thermally controlled chamber to stabilize [87] or modify [113] the ambient experienced by a colony would allow such investigation. Looking ahead, our research aims to harness the platform’s sensing capabilities during the foraging season, specifically to investigate the dynamics of the collective thermoregulation of the broodnest and investigate the potential of inferring population evolution (*i.e.*, demographic forecasting). Furthermore, we are curious to discern whether there are specific thermal cues that can influence the queen’s oviposition location [114].

In this work, we have described the investigative potential of a novel robotic system designed to interact with honeybee colonies, highlighting the broader application of robotics in studying large biological collectives within complex biological contexts. The results of two extensive experiments involving thousands of bees unmistakably demonstrate the promise of this versatile platform for future research, which we hope serves as an inspiration for new systems studying collective thermobiology in other social insects and potentially collectives from more distant taxonomic groups. Our system not only streamlines the automation of conventional experiments but also enables the exploration of unique interactions with biological collectives, with the capacity to enhance our comprehension of animal collective behavior and their ecological interactions.

V. METHODS

A. ANIMALS, COLONIES, AND HIVES

In the course of this investigation, we utilized queenright colonies of *A. mellifera carnica* Pollmann housed in Zander box hives within the Botanical Garden of Graz apiary. Experiments were conducted at the nearby field laboratory ($47^{\circ}4'58.15''\text{N}$, $15^{\circ}27'25.00''\text{E}$), where colonies were transferred from the box hives to observation hives with dimensions $w \times h \times d = 53\text{ cm} \times 68\text{ cm} \times 11\text{ cm}$, which could accommodate two vertical frames. To mimic the dark environment of natural honeybee nests and minimize disturbance, the field laboratory was maintained in darkness. Bees had unrestricted access to the outside via a conduit that connected the hive to the exterior, traversing the field laboratory walls.

This study involved two distinct colonies. One, used in the observation experiment (Sec. III-A), comprised roughly 4000 bees at the start of the experiment. This experiment, which incorporated a robotic device at the bottom part of the hive, spanned 121 days, from 01/08/2020 to 30/11/2020. In the colony position modulation experiment (Sec. III-B), we introduced a second colony with an initial estimated population of 1200 bees. Conducted over 35 days, from 28/12/2022 to 01/02/2023, this experiment utilized two robotic devices situated at the top and bottom sections of the hive. The colonies were fed ad libitum, having free access to a feeder positioned in the upper chamber of the hives. During the warm months, colonies were fed with 73% sucrose solution. During the colder months, the colonies were fed a mixture of 25 parts sucrose, 6 parts honey, and 7 parts water. This composition corresponds to the standard feed mixture according to [115]. Bee welfare was a priority throughout the study; Varroa mite treatments were administered as necessary, even during experimental runs. However, no Varroa treatments were needed during the period of the data presented here.

Under Austrian legislation (Austrian Animal Experiments Act – *Tierversuchsgesetz* 2012-TVG 2012, Section I, §1) and the ethics committee of the University of Graz, insect experimentation does not necessitate ethical approval. The animals involved in this research received continuous care from a professional beekeeper, who also assisted with the experiments and manipulations detailed herein.

B. AUXILIARY SYSTEMS

Diverse supportive devices and procedures were used alongside the robotic system and hives to gather auxiliary data, improve data quality, or store collected data. In this study, imagery played a crucial role in exploring patterns within sensor data streams and understanding the structure and organization of honeybee groups that produced this data (for example Figures 5, 7, and 8). To avoid disrupting the natural darkness within the beehives, we used infrared light illumination, a frequency band invisible to bees [116]. Images were captured by Raspberry Pi High-Quality cameras equipped

with a Sony IMX477 sensor featuring 12.3 megapixels and a 6-mm lens. For each robotic frame installed in an observation hive, two cameras were used, one for each side of the frame. The original acrylic windows of the observation hive were substituted with non-reflective glass to diminish the reflection from infrared illuminators. Each camera was connected to a Raspberry Pi 4 Single-Board Computer (SBC) that managed the shooting interval and stored the images on its SD card. During warmer periods, when the Field Lab experienced significant day-night thermal gradients, the wooden floor's slight expansion or contraction would marginally displace the cameras. To counter this, we attached the observation hives and cameras to a single five-centimeter thick tabletop.

In all experiments presented here, robotic frames were controlled via a Raspberry Pi, which also functioned as a local data storage system, saving all robotic data into text files. Although not essential, this data was periodically transmitted to an InfluxDB time-series database via the Field Lab's wireless network. The database centralized all collected data and facilitated querying the data from multiple colonies [117]. InfluxDB's web interface enabled simple dashboard creation and remote data visualization. For remote control of the robotic frames or database access, the Field Lab network was accessible through an encrypted SSH (Secure Shell) connection.

A weather station (Ecowitt Eurochron EFWS 2900, with temperature precision of 5% and resolution of 0.1 °C) was used to monitor internal and external atmospheric conditions.

C. DATA ANALYSIS

1) STATISTICS

Throughout the text, if not explicitly stated otherwise, metrics of central tendency and dispersion are calculated by the median value and the median absolute difference, MAD, for their robustness against outliers [118]. The values representing measurements' uncertainty depict the combined uncertainty u_c of the systematic and statistical uncertainties of the experimental setup and the observed data set. If not stated otherwise, the uncertainty values are written after the symbol “±” and are calculated by summing in quadrature the instrument(s) uncertainties and the sample set median absolute difference, MAD ($u_c = \sqrt{\text{MAD}^2 + u_{\text{inst}}^2}$). Whenever sensors malfunctioned their data was removed from the analyzed data set. In the observation experiment (Sec. III-A), two sensors malfunctioned (n.31 and 46). During the modulation experiment (Sec. III-B) one sensor (n.63) from the bottom robot also malfunctioned. All data analysis was performed in Python version 3.11.

2) RECREATING THERMAL FIELDS

In the default configuration, the system samples the sensor array every 10 s. The sampling rate can be changed, by users or automated scripts, without interrupting the system. Once the system acquires the temperature values (Fig. 3b), they are transmitted to a controller outside the hive (*e.g.*, another

microcontrolled device, a single-board computer, or a laptop) where data can be further processed and ingested into databases or recorded in files. To reconstruct the thermal fields from the sensor array, we used a radial basis function method [119] to interpolate temperature values in steps of 1 mm.

3) IMAGE PROCESSING

To enhance the quality of the recorded images, a series of treatments were applied, including the correction of distortions introduced by the wide-view lens, adjustment of perspective, cropping to focus on regions of interest, and contrast enhancement through histogram equalization.

D. ETHICS OF MIXING ROBOTS AND BEES

As we previously discussed in [40], interactive robotic systems involve close interactions and information exchange with living animals [13], [120], prompting important ethical considerations. In designing our non-invasive robotic systems and conducting experiments, we aimed to minimize potential adverse effects. For instance, to reduce animal stress, any thermal stimuli emitted by the artificial agents were limited to levels that naturally occur within a bee colony. Since our technology can only be used within managed hives, it will therefore only be in direct contact with honeybees both during and after the device's lifespan. Consequently, its impact on the broader ecosystem is expected to be negligible. However, the effects on the colony and species as a whole should be considered. Our study used managed honeybee colonies. Such bee colonies do not undergo evolutionary adaptation by natural selection. In contrast, their evolution is predominantly shaped by artificial selection following bee-breeding principles [121] for traits like low aggressiveness and high honey yield. If robotics help a weak, perishing colony to thrive and reproduce, its feral offspring without such support would be subject to natural selection, *i.e.*, without any further technological influence. Therefore, we suggest that our robotic systems would have no long-term effects on the evolution of feral honeybees.

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SUPPLEMENTARY MATERIAL

Text with a model describing the heating time of cells containing different materials (Text S1, and Tables S1, S2). Tables with specifications for the humidity (Table S3) and temperature (Table S4) sensor candidates, and figure depicting a replica of the modulation experiment but with actuators at

$T_{obj} = 30^\circ\text{C}$ (Fig. S1). An archive containing design files for hardware, firmware, and software of the system, is available on Zenodo at <https://doi.org/10.5281/zenodo.10908593/>

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