

An automated system for tracking and identifying individual nectar foragers at multiple feeders

Kazuharu Ohashi · Daniel D'Souza · James D. Thomson

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Abstract Nectar-feeding animals have served as the subjects of many experimental studies and theoretical models of foraging. Their willingness to visit artificial feeders renders many species amenable to controlled experiments using mechanical “flowers” that replenish nectar automatically. However, the structural complexity of such feeders and the lack of a device for tracking the movements of multiple individuals have limited our ability to ask some specific questions related to natural foraging contexts, especially in competitive situations. To overcome such difficulties, we developed an experimental system for producing computer records of multiple foragers harvesting from simple artificial flowers with known rates of nectar secretion, using radio frequency identification (RFID) tags to identify individual animals. By using infrared detectors (light-emitting diodes and phototransistors) to activate the RFID readers momentarily when needed, our system prevents the RFID chips from heating up and disturbing the foraging behavior of focal animals. To demonstrate these advantages, we performed a preliminary experiment

with a captive colony of bumble bees, *Bombus impatiens*. In the experiment, two bees were tagged with RFID chips (2.5×2.5 mm, manufactured by Hitachi-Maxell, Ltd., Tokyo, Japan) and allowed to forage on 16 artificial flowers arranged in a big flight cage. Using the resulting data set, we present details of how the bees increased their travel speed between flowers, while decreasing the average nectar crop per flower, as they gained experience. Our system provides a powerful tool to track the movement patterns, reward history, and long-term foraging performance of individual foragers at large spatial scales.

Keywords Artificial flowers · *Bombus* · Foraging · LED sensors · Renewing resources · RFIDs · Spatial use

Introduction

Nectar-feeding animals and their flowers have long been used as a model system for studying the foraging behavior of animals on renewing resources (Gill 1988; Possingham 1988; Possingham 1989; Kadmon 1992; Williams and Thomson 1998; Stout and Goulson 2002). This is because the animals' foraging behavior is readily observable and the quantification of relevant parameters is often tractable. In addition, these animals can be trained to drink nectar from a variety of artificial flowers in enclosures. To take advantage of this, several researchers have developed artificial flowers that replenish automatically, using power-driven nectar pumps (Bertsch 1984; Pflumm 1986; Giurfa 1996; Moffatt 2001; Schilman and Roces 2003) or electromagnetically controlled flowers that draw nectar from a reservoir (Hartling and Plowright 1979; Keasar et al. 1996; Cnaani et al. 2006). In combination with temporal records of visitation patterns, these sophisticated devices have allowed

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K. Ohashi (✉)
Graduate School of Life and Environmental Sciences,
University of Tsukuba,
Tsukuba, Ibaraki 305-8572, Japan
e-mail: kohashi@ies.life.tsukuba.ac.jp

D. D'Souza
6214 Fort Road,
Mississauga, ON, Canada L5V 1X2

J. D. Thomson
Department of Ecology and Evolutionary Biology,
University of Toronto,
25 Harbord Street,
Toronto, ON, Canada M5S 3G5

experimenters to estimate the standing crop of nectar a flower at any one time. This key parameter is essentially impossible to measure with real flowers in the field.

In principle, replenishing flowers can be used to explore the same range of topics as in field studies. However, two prevailing features of such designs have greatly limited our ability to address some specific questions, such as whether and how spatial distributions of flowers, movement patterns, and competition with others would affect the foraging performance of an animal (Ohashi and Thomson 2005). First, replenishing flowers may be too costly and mechanically complex to deploy in large numbers (Cresswell and Smithson 2005). Second, previous flowers have never been outfitted with a device to track multiple foragers individually, although infrared light detectors have been used to record visits by solo foragers at multiple replenishing feeders (Moffatt 2001).

Therefore, we have developed an automated system for tracking and identifying individual bumble bees competing for nectar from multiple feeders, by combining relatively foolproof flowers that secrete nectar continuously and a digital tagging technology called radio frequency identification (RFID). Previous authors have demonstrated that RFID chips can be applied to social insects and used to monitor the individuals going in and out with readers placed at the nest entrances (ants—Robinson et al. 2009; bumble bees—Streit et al. 2003; Molet et al. 2008; paper wasps—Sumner et al. 2007). However, these small chips are usually passive (non-battery powered) and capture all their energy from interrogation signals emitted by the readers (Sarma et al. 2002; Want 2004). When a chip receives a signal from the reader, therefore, it inevitably dissipates a significant amount of heat. This would not seem to pose a problem when the interrogation zone is located at a nest entranceway through which animals pass quickly. If readers are located at feeders where animals stay for a few seconds or longer, however, continuously interrogated chips would be more likely to accumulate heat, particularly if the chips do not fully cool during flights between feeders. Such heating could plausibly affect the foraging behavior in question. In other contexts, a temperature rise of several degrees Celsius in flowers—caused by sun-tracking movements or thermogenesis—can be perceived by endothermic insects (diptera, beetles, bumble bees, etc.) as a metabolic reward and can induce a visit preference or an extended stay, even in the absence of a nutritional reward (Kevan 1975; Seymour et al. 2003; Dyer et al. 2006). We avoided this problem by adding infrared light-emitting diodes (LEDs) and phototransistors (IR detectors) to the system, so that individual readers send signals only for a moment when a visitor is detected. Here, we describe details of our system and demonstrate how the system was used to track foraging behavior and perfor-

mance of pairs of competing workers of bumble bees, *Bombus impatiens*.

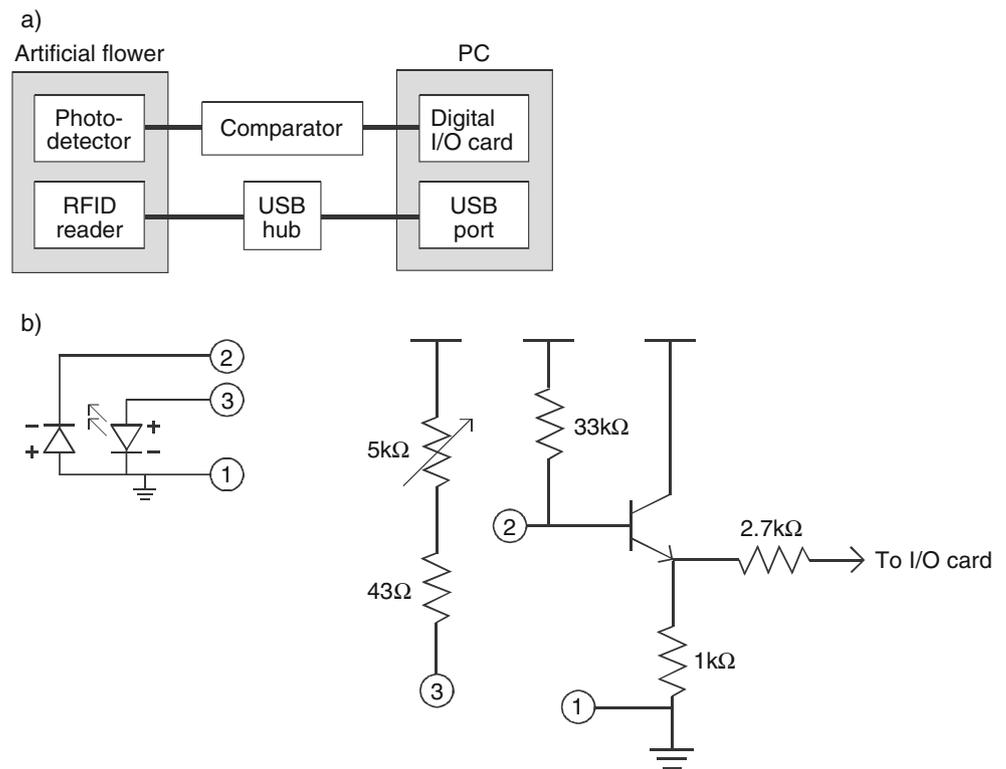
System description

The entire system comprises both instrumentation and software (Fig. 1). The artificial flowers, IR detectors, and the RFID readers make up the instrumentation, while data are logged via software. The artificial flower is a purely mechanical system whose only function is to provide each station with a steady stream of nectar. The IR detector and the RFID reader are electronic subsystems that serve as inputs to a personal computer. The data logger is a software system that runs on PC, and gathers data based on the inputs from IR detectors and RFID readers.

Artificial flowers

Figure 2 shows the design of the artificial flowers. Each flower is a vertical box made of clear acrylic plastic with a horizontal platform (flower stage) halfway up the box (Fig. 2a). The top lid and the upper half of the front wall are detachable, allowing easy access to the mechanism. A small electric clock motor, mounted at the top of the box, turns an axle at 1/30 rpm. The turning axle winds up a thread that is clipped to one end of a flexible reservoir: a 50 cm length of flexible tubing, 3.0 mm in internal diameter, that contains sucrose solution (nectar). The other end of the tube terminates in a steel needle inserted into a “flower,” comprising a “nectar bucket” (a hole 5.5 mm in diameter, 7.0 mm in depth) drilled in the flower stage (Fig. 2b). As the motor lifts the reservoir, the nectar oozes out through the needle and accumulates in the bucket at a constant rate (e.g., 1.8 $\mu\text{l}/\text{min}$ with a 2.4-mm-diameter axle). Using a fine nylon thread minimizes the possibility that the thread winds on top of itself and increases the effective diameter of the axle; with a 2.4-mm-diameter axle, the thread seldom or never overlaps for the first 7 h, which is long enough for normal daily experiments. A thin plastic baffle prevents the bees from getting excess nectar directly from the steel needle hole, so the bees have access only to the nectar accumulated at the bottom. Each nectar bucket is topped with a U-shaped block of plastic, painted blue for easy detection by bees. As bees enter the U to extract nectar, they pass under a Hitachi-Maxell Reader/Writer module that reads individual RFID chips as bees enter the flower (Fig. 2c, d; see also “Monitor system”). The module also serves as a barrier that prevents bees from directly reaching the bucket without breaking the infrared light beam at the entrance. When the experiment continues for more than 7 h or the clip is pulled to the top, we unwind the thread and refill the tube with nectar using a wash bottle. To allow

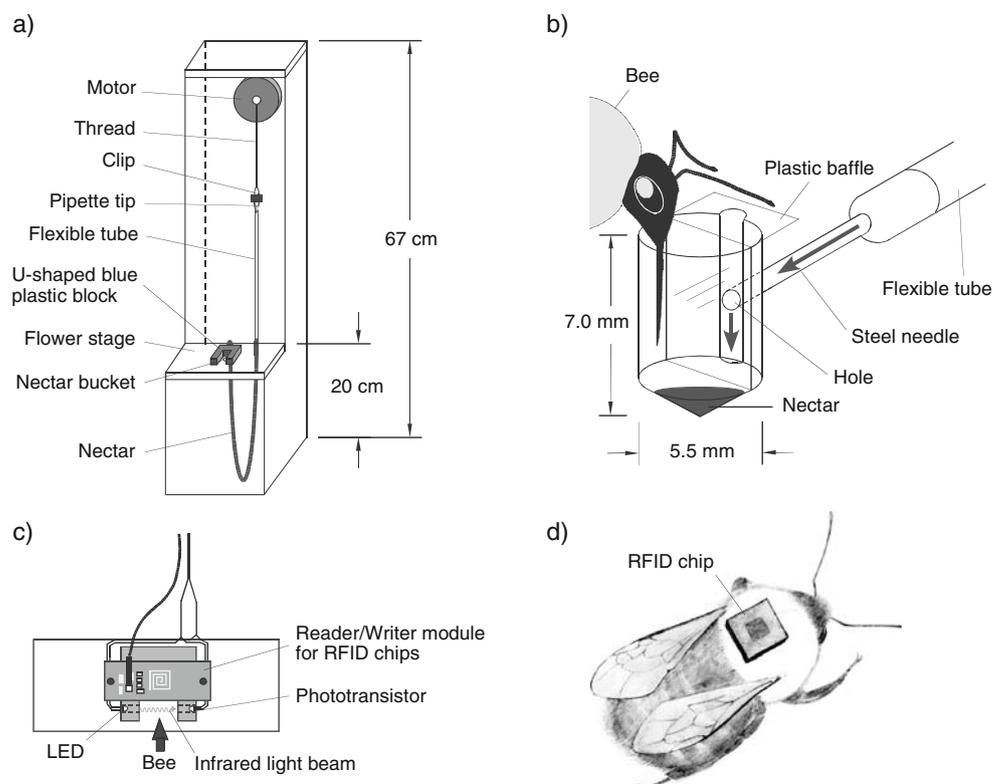
Fig. 1 Diagrams of the system. **a** Block diagram for the entire system with one artificial flower and **b** circuit diagram for one channel of IR detection system



easier refilling of the nectar and to avoid pinching off the tube, we cut a pipette tip (a standard yellow tip for 200 μ l) in half and glued the thicker half to the end of the tube as a funnel and clipping surface.

Although the design of our flower is intentionally simple and tuned for specific experimental conditions with *B. impatiens*, it can be readily modified for other experiments. First, the number of flower stages or the number of nectar

Fig. 2 Views of the artificial flowers. **a** A whole view; **b** a close-up view of the nectar bucket; **c** a top view of the U-shaped block embedded with an IR detector and RFID reader; and **d** a worker of *Bombus impatiens* tagged with an RFID chip



buckets per stage could be increased to simulate a multi-flowered or a spatially structured inflorescence. Second, the rate of nectar secretion can be adjusted by changing the diameter or the turning axle (Ohashi et al. 2007; Ohashi et al. 2008) or by adopting a circuitry that runs the motor intermittently (e.g., 2 s out of 4 s). If much slower rates of discharge are required, as is often the case with multi-flowered patches or plants (Giurfa 1996; Moffatt 2001), one could replace the simple axle with a "differential windlass" (Chopra 2002), in which two cylinders of slightly different diameter rotate around the same axis with a single coil of thread wound in opposite directions on each—the thread winds onto the thicker cylinder as it winds off the thinner, giving a very slow lifting of the central loop. For example, if the diameters of the two cylinders differ by 1.0 mm, the loop would be lifted 4.4 mm per hour and give 0.37 $\mu\text{l}/\text{min}$ of nectar secretion. Because the lifting speed simply depends on the size difference between the two cylinders, one can also avoid the problem of overlapping thread by using thick cylinders. Third, one can extend the two arms of the U-shaped block (i.e., the length of the tunnel) to increase handling time per flower. Finally, the measurements of the nectar bucket and the U-shaped block can be adjusted to the body shapes or tongue lengths of different animals.

Monitor system

Each flower is equipped with an IR detector at its opening, which consists of an infrared LED and a phototransistor that work together as an optocouple (Fig. 2c). An infrared LED produces a beam that is sensed by a phototransistor. When a bee crawls through the tunnel, it interrupts the beam and produces a signal on the phototransistor output. The important requirement for such an optocouple pair is to have a threshold value to compare against, in order to determine whether or not a bee is at the flower. For ease of use, we decided to have the threshold permanently fixed in the hardware and leave only the light source intensity adjustable. This permits the experimenter to compensate for lab lighting conditions, tolerances in the electronic components, and possible variances in the construction of each module. The hardware threshold was set high enough so that direct sunlight would register as a blocked beam. This prevents the sun from falsely indicating a permanently vacant flower. The experimenter has to compensate by turning up the intensity of infrared LEDs to bias the system by holding the output of phototransistors above the threshold. The IR detectors are all connected to a central control box where the main power source for the IR system is connected and the intensities of infrared LEDs are adjusted. The control box also serves to connect the hardware to the PC via a digital input/output card (DIO

card). The control box receives the analog signal from the phototransistor and converts it to the appropriate electrical levels that the DIO card requires. All circuitry other than the readers, the infrared LEDs, and the phototransistors is contained centrally in the control box.

When the computer receives the signal from the phototransistor, the software immediately maps the RFID reader for the flower and interrogates a tag (passive 2.5-mm square RFID chip [the Coil-on-Chip RFID system[®], Hitachi-Maxell, Ltd., Tokyo, Japan]) bonded to the bee's thorax with gel-type cyanoacrylate adhesive (Instant Crazy Glue[®] All Purpose Gel, Crazy Glue, Columbus, Ohio, USA; Fig. 2d). The RFID readers communicate with the software via USB. Due to the design of the USB protocols, each RFID reader is assigned an ID in an unpredictable manner. This means that, every time the system is started, the RFID readers lose synchronization with their associated IR detector, and that the system needs to be calibrated through a setup routine: the experimenter manually blocks the IR detector of each flower and provides the RFID reader with a chip to read. Once the software detects the blockage, it cycles through all the RFID readers one at a time until a chip is read. When a reader is found that responds with a chip number, the RFID reader is assigned with a serial number (flower ID) to the IR detector that initiated that search cycle. The experimenter continues this procedure for every flower in the array. Once calibrated, the software receives the signal from the hardware by reading data from RAM, which is mapped to a known address by the DIO card. The software checks for any change in data at that location. When the change indicates that a bee has arrived at the flower (i.e., the beam is masked), the software issues the command to the RFID reader to send an electromagnetic pulse to read the bee's RFID-chip number (bee ID). Because the reader is activated only momentarily, the interrogated RFID chip does not heat up even if the bee stays for a few seconds or longer. When the change indicates that the bee has vacated the flower (i.e., the beam is reconnected), then the flower ID, the bee ID, and the arrival and departure time (to 0.1 s) are logged to a data file. The resulting data file thus contains flower ID, bee ID, and arrival and departure time for each visitation in a sequence. The software graphically displays the spatial layout of flowers and the bee IDs at flowers they are currently detected, so that the experimenter can keep track of multiple bees' movement in real time on the PC screen.

Proof of concept

To demonstrate the feasibility and advantages of our system, we tagged a number of workers from a commercial colony of *B. impatiens* Cresson (supplied by Biobest,

Leamington, Ontario, Canada) and allowed them to visit and collect 30% sucrose solution (*w/w*) from an array of the artificial flowers in an indoor cage (788×330×200 cm). The array consisted of 16 artificial flowers arranged in a diamond shape, with nearest neighbors spaced 0.95 m from each other (Ohashi et al. 2008). We had verified during the process of development that our monitor system could keep track of five to ten simultaneous foragers. With such high visitation rates, however, bees encountered so many empty flowers that they often lost their motivation to forage. We, therefore, conducted pilot studies with only one pair of tagged foragers. These bees shuttled between the hive and the array actively and continually.

The two bees were allowed to forage freely in the cage while the system was turned on. When each bee was filled up and returned to the hive to deposit its nectar load, we manually annotated the computer file that the first trip for that bee was done, and waited until it re-emerged. Similarly, the accumulated number of foraging trips made by each bee was manually annotated every time it went back to the hive. When both bees were back in the hive or inactive in the cage, we occasionally stopped the electric motors for the artificial flowers to prevent nectar overflow. To integrate a record of such on/off timing of the motors into the data file, we used an additional U-shaped block with an IR detector and manually interrupted the beam while we turned the motors on. The trial was continued until each bee made 60 foraging trips, which took 5–6 h. Similar procedures have been described in more detail by Ohashi et al. (2008).

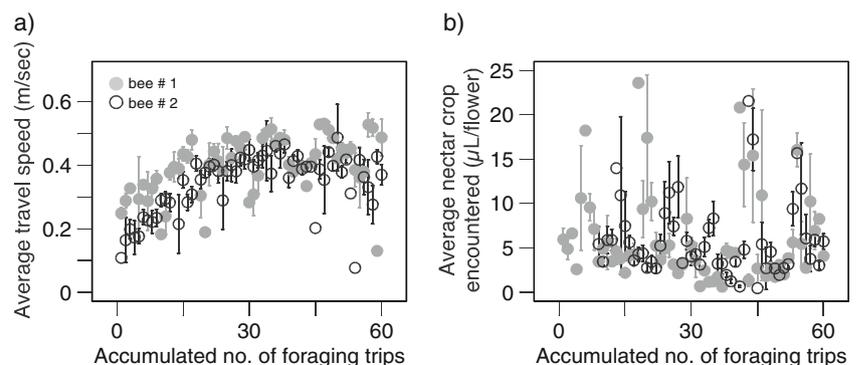
The recorded data occasionally contained two or more immediately successive visits to the same flower by the same bee. These represented temporary reconnection of the beam caused by bees adopting anomalous postures in the tunnel or briefly departing from the flower. We regarded such records as one single visit and added up their probing times. We confirmed that the visitation sequences obtained from such data editing procedures completely matched with those from direct observations. We also double-checked that the IR detectors could keep

track of successive visitations throughout the data collection by monitoring the real-time graphical displays on the PC screen. We subsequently estimated the amount of nectar a bee gained at each visit, assuming that (1) nectar accumulated in flowers with time at a constant rate (1.8 $\mu\text{l}/\text{min}$) as long as the motors were running, (2) all the accumulated nectar was taken by a bee at one visit, and (3) nectar secreted while probing was also taken by the bee. Although we carefully drained accumulated nectar from all nectar buckets with a syringe beforehand, the bees' probing behavior suggested that small amounts of nectar remained for the initial few visits. As a precautionary measure, therefore, we omitted nectar crops encountered at the initial two visits to each flower (after the motor was first turned on for the day).

To demonstrate the power of the system, we present two examples of possible questions: how did bees change their average travel speed between flowers, and how did they change the average nectar crop per flower, as they accumulated foraging experience from trip to trip? We arbitrarily designate the two bees as bee #1 and bee #2. Both bees increased their travel speed between flowers in a decelerating way as they gained experience, and bee #1 traveled faster than #2 throughout the day (Fig. 3a). On the other hand, the bees slightly decreased the average nectar crop per flower as they gained experience and speed, and the difference in average nectar crop between the two bees was trivial (Fig. 3b). The gross rate of nectar intake (=total amount of nectar gain divided by total time spent on interflower movements and probing flowers) was higher in bee #1 (16.2 $\mu\text{l}/\text{min}$) than in #2 (14.4 $\mu\text{l}/\text{min}$) due to the difference in their travel speed. One can perform further analyses to ask whether this outcome was a result of differences between the bees in the geometry of their foraging paths, temporal patterns of visitation at each flower, or the spatial and temporal overlaps with the competitor, etc. Clearly, the system has the potential to provide detailed records of how the foraging experiences of multiple bees interact through time.

Fig. 3 Changes in behavior of simultaneous foragers with accumulated experience.

a Travel speed between flowers and **b** nectar crop per flower. Mean \pm SE were calculated for each trip using data written in a computer file



Limitations and suggestions for further improvement

There are still a few limitations to be addressed concerning the design of RFID and flowers. First, the RFID readers occasionally failed to detect bee identities properly. In such cases (normally, <10% of total visits), the software would write "0000000" as the bee ID, while the IR detector still timed the visitation without fail. These misreads of the bee ID arose when bees atypically ducked below the beam in the tunnel or when they departed from the flower immediately after their arrival; due to the limitation of low carrier frequency for such small readers and chips (13.56 MHz), the chip must come to within 2.4 mm from the reader to be detected. To address this problem, we have written computer programs to infer the missing bee IDs from spatially and temporally adjacent records. Because a bee's movement is limited by its flight speed and the distance between flowers, we could usually identify a single possible candidate for each of these visits. For rare cases that remained ambiguous, we would omit the records from the data set by treating the ambiguous portion as an interruption of the recording process. This problem may be effectively solved if newer chip designs extend the minimum distance required between the reader and the chip.

Second, the system occasionally registered only one visit when two bees were actually at a single flower simultaneously, pushing past or on top of one another. If the second bee's ID failed to register, the apparent single visit would be unnaturally long, and would be attributed to the first bee. This could lead a slight misestimation of the reward crop encountered. As is often the case with bumble bees and their flowers in the field, such bee–bee encounters were infrequent (2% of visits at the highest) in our experimental setup. When working with more crowded, unnatural situations, however, this could be a bigger problem. The best solution would be more restrictive flowers that only allow one bee to enter at a time; alternatively, direct video observation might be necessary.

Finally, the current system has not been equipped with a device to control the replenishment schedule of nectar in flowers. For example, it might be more realistic if each flower automatically stops its nectar secretion at a certain level as some real flowers do (Castellanos et al. 2002). This could be achieved by adding a computer program to control the flow of electricity, so that it would stop the motor when the inter-arrival time at the flower runs past a set limit, and reactivate the motor after a visit occurs. Although nonlinear nectar replenishment can also be simulated by a much simpler feeder with a silk thread that draws nectar from a reservoir by capillary action (Makino and Sakai 2007), the design of an electronically controllable "maximum crop" would give great scope for future studies.

Conclusion

By combining RFID-based identification technology and LED-based detection technology, our system allows several hours of automated recording of arrival and departure time of successive visits of multiple bees in an array of artificial flowers. The artificial flowers secrete nectar at a known, continuous rate, so that standing crops of nectar can be calculated at any moment. We have shown that this system can be a powerful tool for analyzing animal foraging behavior on renewable resources, such as time-course changes in the patterns of spatial movement, reward encountered at each flowers, and average nectar intake per unit of time.

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Contributions of authors J.D.T. conceived and designed the original motorized artificial flowers for continuous nectar secretion. K.O. refined the mechanical aspects of artificial flowers so that a bee can obtain only a small amount of nectar at once. D.D., K.O., and J.D.T. devised the monitor system. D.D. built the monitor system, including both instrumentation and software. K.O. and J.D.T. planned and performed the preliminary experiments. All authors read and approved the final manuscript.

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