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METHODS

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

Kazuharu Ohashi^a, Daniel D'Souza^b, and James D. Thomson^c

^a Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

^b 6214 Fort Road, Mississauga, Ontario, Canada L5V 1X2

^c Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, Ontario, Canada M5S 3G5

Correspondence: K. Ohashi

Email: kohahsi@ies.life.tsukuba.ac.jp

Running title: Automated tracking of individual foragers at multiple feeders

27 **Abstract**

28 Nectar-feeding animals have served as the subjects of many experimental studies and theoretical models of
29 foraging. Their willingness to visit artificial feeders renders many species amenable to controlled
30 experiments using mechanical “flowers” that replenish nectar automatically. However, the structural
31 complexity of such feeders and the lack of a device for tracking the movements of multiple individuals have
32 limited our ability to ask some specific questions related to natural foraging contexts, especially in
33 competitive situations. To overcome such difficulties, we developed an experimental system for producing
34 computer records of multiple foragers harvesting from simple artificial flowers with known rates of nectar
35 secretion, using radio-frequency identification (RFID) tags to identify individual animals. By using infrared
36 detectors (LEDs and phototransistors) to activate the RFID readers momentarily when needed, our system
37 prevents the RFID chips from heating up and disturbing the foraging behavior of focal animals. To
38 demonstrate these advantages, we performed a preliminary experiment with a captive colony of bumble bees,
39 *Bombus impatiens*. In the experiment, two bees were tagged with RFID chips (2.5 x 2.5 mm, manufactured
40 by Hitachi-Maxell, Ltd., Tokyo, Japan) and allowed to forage on 16 artificial flowers arranged in a big flight
41 cage. Using the resulting data set, we present details of how the bees increased their travel speed between
42 flowers, while decreasing the average nectar crop per flower, as they gained experience. Our system
43 provides a powerful tool to track the movement patterns, reward history, and long-term foraging
44 performance of individual foragers at large spatial scales.

45

46 **Key-words** Artificial flowers, *Bombus*, Foraging, LED sensors, Renewing resources, RFIDs, Spatial use

47 **Introduction**

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

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

67 Therefore, we have developed an automated system for tracking and identifying individual
68 bumble bees competing for nectar from multiple feeders, by combining relatively foolproof flowers that
69 secrete nectar continuously and a digital tagging technology called RFID (radio frequency identification).
70 Previous authors have demonstrated that RFID chips can be applied to social insects and used to monitor the
71 individuals going in and out with readers placed at the nest entrances (ants: Robinson et al. 2009; bumble
72 bees: Streit et al. 2003; Molet et al. 2008; paper wasps: Sumner et al. 2007). However, these small chips are
73 usually passive (non-battery powered) and capture all their energy from interrogation signals emitted by the

74 readers (Sarma et al. 2002; Want 2004). When a chip receives a signal from the reader, therefore, it
75 inevitably dissipates a significant amount of heat. This would not seem to pose a problem when the
76 interrogation zone is located at a nest entranceway through which animals pass quickly. If readers are
77 located at feeders where animals stay for a few seconds or longer, however, continuously interrogated chips
78 would be more likely to accumulate heat, particularly if the chips do not fully cool during flights between
79 feeders. Such heating could plausibly affect the foraging behavior in question. In other contexts, a
80 temperature rise of several degrees C in flowers — caused by sun-tracking movements or thermogenesis —
81 can be perceived by endothermic insects (diptera, beetles, bumble bees, etc.) as a metabolic reward and can
82 induce a visit preference or an extended stay, even in the absence of a nutritional reward (Kevan 1975;
83 Seymour et al. 2003; Dyer et al. 2006). We avoided this problem by adding infrared light emitting diodes
84 and phototransistors (IR detectors) to the system, so that individual readers send signals only for a moment
85 when a visitor is detected. Here we describe details of our system, and demonstrate how the system was used
86 to track foraging behavior and performance of pairs of competing workers of bumble bees, *Bombus*
87 *impatiens*.

88

89 **System description**

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

96

97 *Artificial flowers*

98 Figure 2 shows the design of the artificial flowers. Each flower is a vertical box made of clear acrylic plastic
99 with a horizontal platform (flower stage) halfway up the box (Fig. 2a). The top lid and the upper half of the
100 front wall are detachable, allowing easy access to the mechanism. A small electric clock motor, mounted at

101 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
102 a flexible reservoir: a 50 cm length of flexible tubing, 3.0 mm in internal diameter, that contains sucrose
103 solution (nectar). The other end of the tube terminates in a steel needle inserted into a “flower,” comprising a
104 “nectar bucket” (a hole 5.5 mm in diameter, 7.0 mm in depth) drilled in the flower stage (Fig. 2b). As the
105 motor lifts the reservoir, the nectar oozes out through the needle and accumulates in the bucket at a constant
106 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
107 the thread winds on top of itself and increases the effective diameter of the axle; with a 2.4-mm diameter
108 axle, the thread seldom or never overlaps for the first seven hours, which is long enough for normal daily
109 experiments. A thin plastic baffle prevents the bees from getting excess nectar directly from the steel needle
110 hole, so the bees have access only to the nectar accumulated at the bottom. Each nectar bucket is topped with
111 a U-shaped block of plastic, painted blue for easy detection by bees. As bees enter the U to extract nectar,
112 they pass under a Hitachi-Maxell Reader/Writer module that reads individual RFID chips as bees enter the
113 flower (Fig. 2c, d; see also "Monitor system"). The module also serves as a barrier that prevents bees from
114 directly reaching the bucket without breaking the infrared light beam at the entrance. When the experiment
115 continues for more than seven hours or the clip is pulled to the top, we unwind the thread and refill the tube
116 with nectar using a wash bottle. To allow easier refilling of the nectar, and to avoid pinching off the tube, we
117 cut a pipette tip (a standard yellow tip for 200 μL) in half and glued the thicker half to the end of the tube as
118 a funnel and clipping surface.

119 Although the design of our flower is intentionally simple and tuned for specific experimental
120 conditions with *Bombus impatiens*, it can be readily modified for other experiments. First, the number of
121 flower stages or the number of nectar buckets per stage could be increased to simulate a multi-flowered or a
122 spatially structured inflorescence. Second, the rate of nectar secretion can be adjusted by changing the
123 diameter or the turning axle (Ohashi et al. 2007; Ohashi et al. 2008) or by adopting a circuitry that runs the
124 motor intermittently (e.g., two seconds out of four). If much slower rates of discharge are required, as is
125 often the case with multi-flowered patches or plants (Giurfa 1996; Moffatt 2001), one could replace the
126 simple axle with a "differential windlass" (Chopra 2002), in which two cylinders of slightly different
127 diameter rotate around the same axis with a single coil of thread wound in opposite directions on each — the

128 thread winds onto the thicker cylinder as it winds off the thinner, giving a very slow lifting of the central
129 loop. For example, if the diameters of the two cylinders differ by 1.0 mm, the loop would be lifted 4.4 mm
130 per hour and give $0.37 \mu\text{l}/\text{min}$ of nectar secretion. Because the lifting speed simply depends on the size
131 difference between the two cylinders, one can also avoid the problem of overlapping thread by using thick
132 cylinders. Third, one can extend the two arms of the U-shaped block (i.e., the length of the tunnel) to
133 increase handling time per flower. Finally, the measurements of the nectar bucket and the U-shaped block
134 can be adjusted to the body shapes or tongue lengths of different animals.

135

136 *Monitor system*

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

154 When the computer receives the signal from the phototransistor, the software immediately maps

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

176

177 **Proof of concept**

178 To demonstrate the feasibility and advantages of our system, we tagged a number of workers from a
179 commercial colony of *Bombus impatiens* Cresson (supplied by Biobest, Leamington, Ontario, Canada), and
180 allowed them to visit and collect 30 % sucrose solution (w/w) from an array of the artificial flowers in an
181 indoor cage (788 x 330 x 200 cm). The array consisted of 16 artificial flowers arranged in a diamond shape,

182 with nearest neighbors spaced 0.95 m from each other (Ohashi et al. 2008). We had verified during the
183 process of development that our monitor system could keep track of 5 to 10 simultaneous foragers. With
184 such high visitation rates, however, bees encountered so many empty flowers that they often lost their
185 motivation to forage. We therefore conducted pilot studies with only one pair of tagged foragers. These bees
186 shuttled between the hive and the array actively and continually.

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

196 The recorded data occasionally contained two or more immediately successive visits to the same
197 flower by the same bee. These represented temporary reconnection of the beam caused by bees adopting
198 anomalous postures in the tunnel or briefly departing from the flower. We regarded such records as one
199 single visit and added up their probing times. We confirmed that the visitation sequences obtained from such
200 data editing procedures completely matched with those from direct observations. We also double-checked
201 that the IR detectors could keep track of successive visitations throughout the data collection, by monitoring
202 the real-time graphical displays on the PC screen. We subsequently estimated the amount of nectar a bee
203 gained at each visit, assuming that i) nectar accumulated in flowers with time at a constant rate ($1.8 \mu\text{L}/\text{min}$)
204 as long as the motors were running, ii) all the accumulated nectar was taken by a bee at one visit, and iii)
205 nectar secreted while probing was also taken by the bee. Although we carefully drained accumulated nectar
206 from all nectar buckets with a syringe beforehand, the bees' probing behavior suggested that small amounts
207 of nectar remained for the initial few visits. As a precautionary measure, therefore, we omitted nectar crops
208 encountered at the initial two visits to each flower (after the motor was first turned on for the day).

209 To demonstrate the power of the system, we present two examples of possible questions: how
210 did bees change their average travel speed between flowers, and how did they change the average nectar
211 crop per flower, as they accumulated foraging experience from trip to trip? We arbitrarily designate the two
212 bees as bee #1 and bee #2. Both bees increased their travel speed between flowers in a decelerating way as
213 they gained experience, and bee #1 traveled faster than #2 throughout the day (Fig. 3a). On the other hand,
214 the bees slightly decreased the average nectar crop per flower as they gained experience and speed, and the
215 difference in average nectar crop between the two bees was trivial (Fig. 3b). The gross rate of nectar intake
216 (= total amount of nectar gain divided by total time spent on interflower movements and probing flowers)
217 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
218 can perform further analyses to ask whether this outcome was a result of differences between the bees in the
219 geometry of their foraging paths, temporal patterns of visitation at each flower, or the spatial and temporal
220 overlaps with the competitor, etc. Clearly, the system has the potential to provide detailed records of how the
221 foraging experiences of multiple bees interact through time.

222

223 **Limitations and suggestions for further improvement**

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

236 chip.

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

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

253

254 **Conclusion**

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

262

263 **Acknowledgements**

264 Chad Brassil first suggested the use of radio-tagging technology for tracking and identification of bees. Alex
265 Fujiwara and Toshiyuki Kaneko (Hitachi Maxell Corporation) provided the product specifications of the
266 Coil-on-Chip RFID system[®] required for developing the data acquisition system. Alison Leslie helped us
267 improve the design of flowers and perform data collection. Luu Trung crafted the artificial flowers. Useful
268 discussion and invaluable help have been contributed by James Burns, Jonathan Cnaani, Robert Gegear, and
269 Michael Otterstatter also contributed to the development of our idea. Biobest provided a commercial colony
270 of *Bombus impatiens*. Two anonymous reviewers made useful comments on the manuscript. This research
271 was supported by a fellowship of the Japan Society for the Promotion of Science for Research Abroad and
272 Grant-in-Aid for Young Scientists (B) to K.O. and grants from the Natural Sciences and Engineering
273 Research Council of Canada, the Canada Foundation for Innovation, and the Ontario Innovation Trust to
274 J.D.T.

275

276 **Contributions of authors**

277 JDT conceived and designed the original motorized artificial flowers for continuous nectar secretion. KO
278 refined the mechanical aspects of artificial flowers so that a bee can obtain only a small amount of nectar at
279 once. DD, KO, and JDT devised the monitor system. DD built the monitor system, including both
280 instrumentation and software. KO and JDT planned and performed the preliminary experiments. All authors
281 read and approved the final manuscript.

282

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343 and foraging success at single plants. *Behavioral Ecology* 9:612-621
344

344 **Figure legends**

345 Fig. 1 — Diagrams of the system. (a) Block diagram for the entire system with one artificial flower and (b)
346 circuit diagram for one channel of IR detection system.

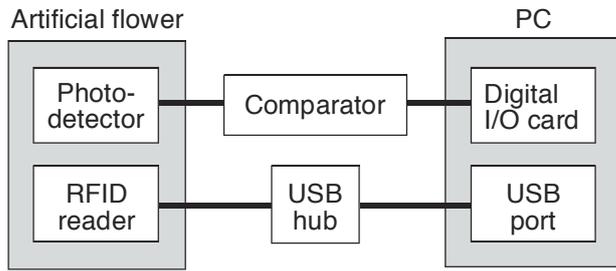
347

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

351

352 Fig. 3 — Changes in behavior of simultaneous foragers with accumulated experience. (a) Travel speed
353 between flowers and (b) nectar crop per flower. Mean \pm SE were calculated for each trip using data
354 written in a computer file.

a)



b)

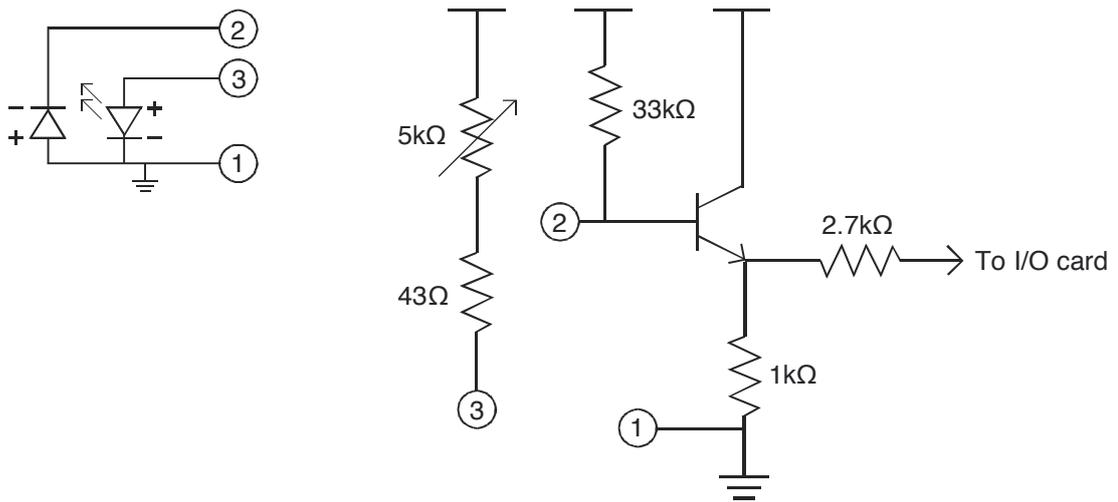
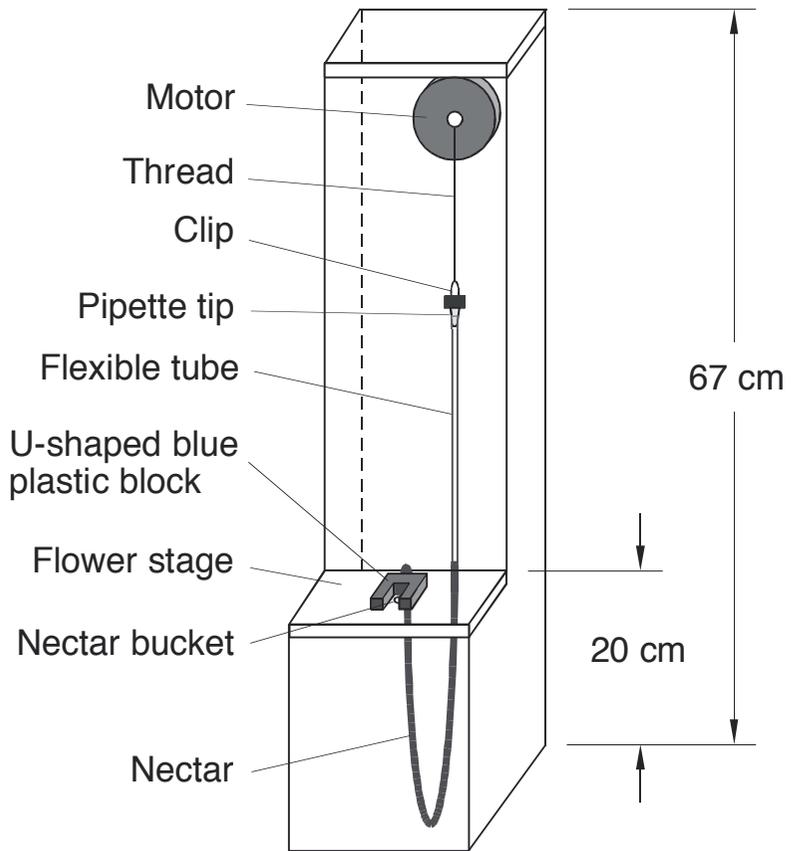


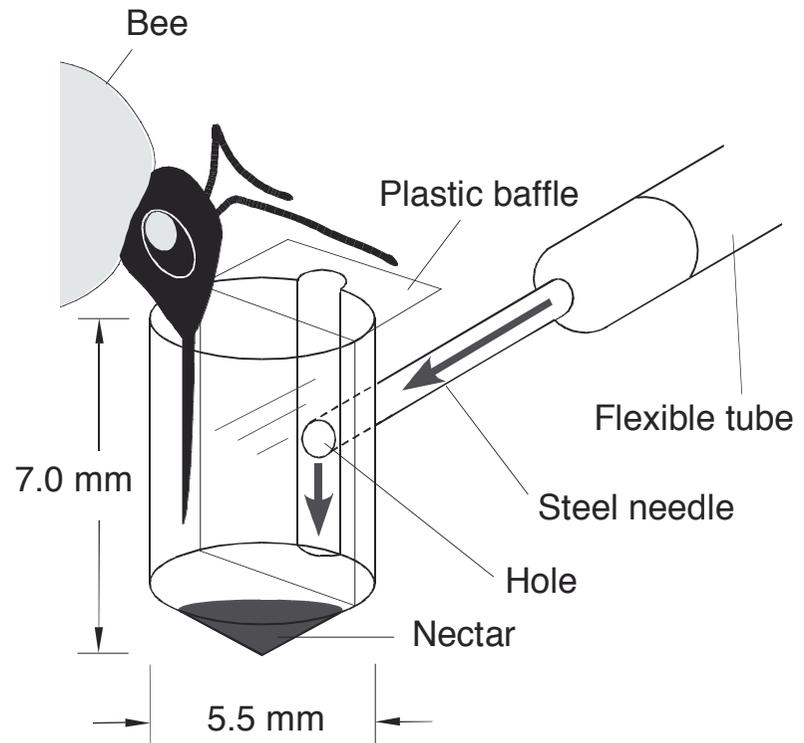
Figure 1

Figure 2

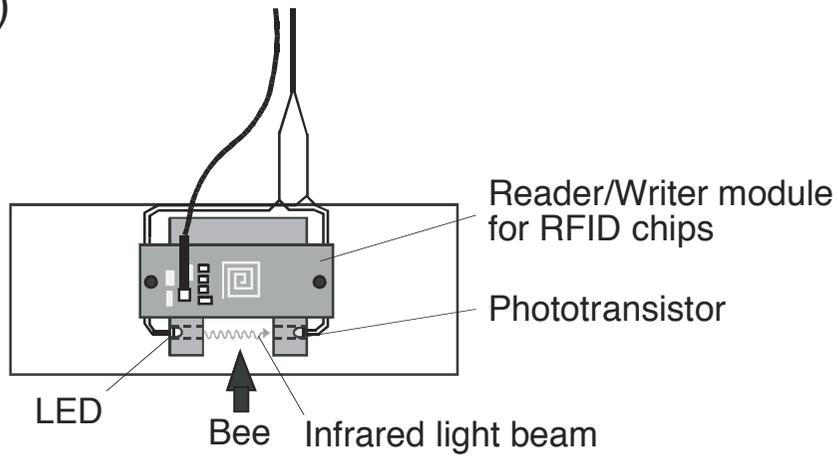
a)



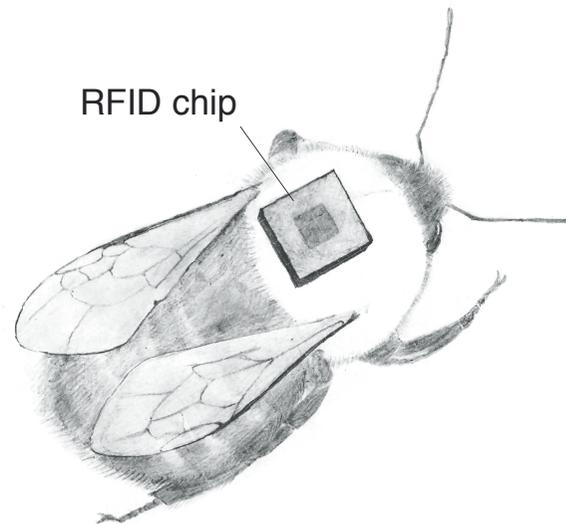
b)



c)



d)



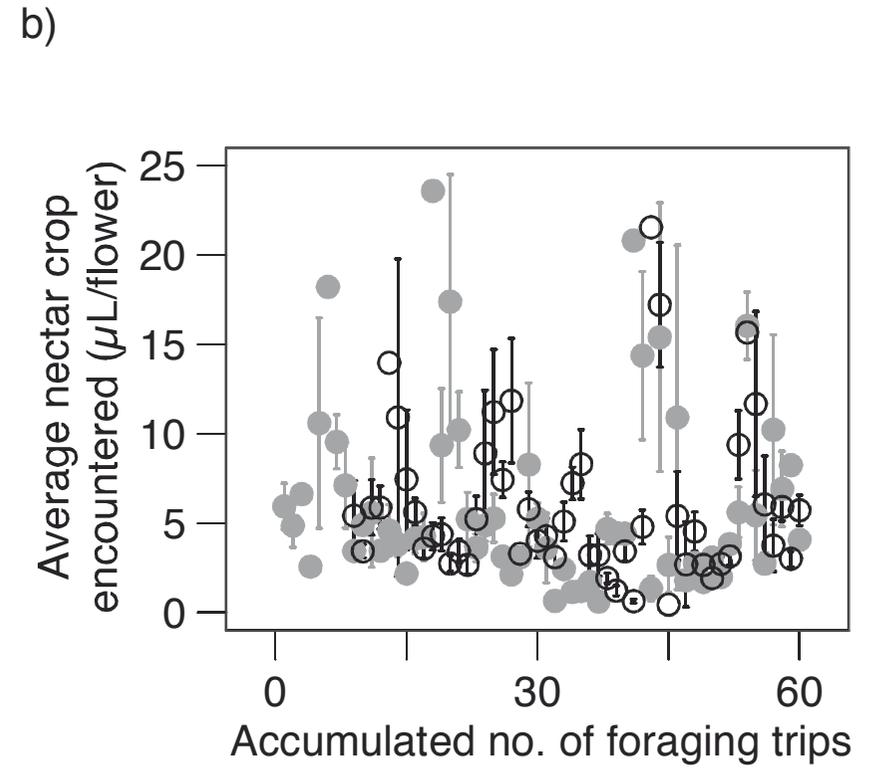
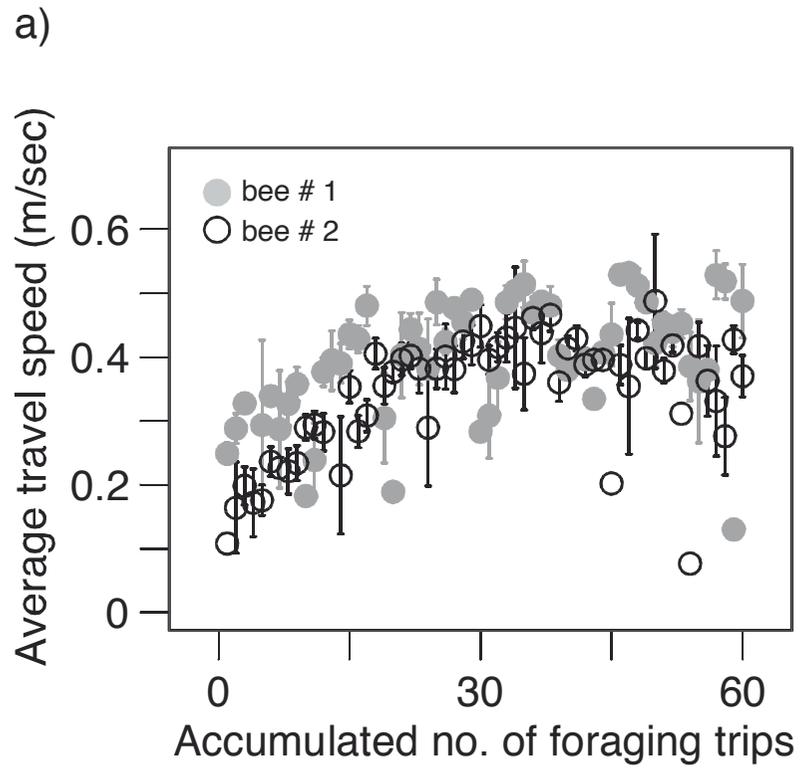


Figure 3