

Speed-Accuracy Tradeoffs and False Alarms in Bee Responses to Cryptic Predators

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Summary

Learning plays a crucial role in predator avoidance [1–3], but little is known about how the type of experience with predators molds future prey behavior. Specifically, is predator-avoidance learning and memory retention disrupted by cryptic coloration of predators, such as crab spiders [4, 5]? How does experience with different predators affect foraging decisions? We evaluated these questions by exposing foraging bumblebees to controlled predation risk from predators (robotic crab spiders) that were either cryptic or highly contrasting, as assessed by a quantitative model of bee color perception [6]. Our results from 3D tracking software reveal a speed-accuracy tradeoff [7]: Bees slow their inspection flights after learning that there is a risk from cryptic spiders. The adjustment of inspection effort results in accurate predator detection, leveling out predation risk at the expense of foraging time. Overnight-retention tests reveal no decline in performance, but bees that had experienced cryptic predators are more prone to “false alarms” (rejection of foraging opportunities on safe flowers) than those that had experienced conspicuous predators. Therefore, bees in the cryptic-spider treatment made a functional decision to trade off reduced foraging efficiency via increased inspection times and false-alarm rates against higher potential fitness loss from being injured or eaten.

Results and Discussion

It is well known that animals, including bees, learn to balance predation threat and potential foraging gains [8–11]. However, detection and subsequent avoidance of cryptic predators, including crab spiders that can change color to match their background [4, 5], pose intriguing challenges with respect to the relative investments into decision speed and accuracy, as well as the minimization of false-negative responses, in which overcautiousness might compromise the range of available foraging options. In our experiments, we presented nectar-foraging bumblebees with an array of yellow artificial flowers harboring either cryptic (yellow) or conspicuous (white) spider models. Conspicuous white spiders present a more salient visual signal to associate with danger than cryptic yellow spiders because white spiders on yellow flowers constitute a highly contrasting color signal to bees (Figure S1 available online). Conversely, the color contrast of cryptic yellow spiders on yellow flowers used in our experiments is below the limit [12] that can easily be discriminated by bees (Figure S1), so

they must rely on shape cues presented by the shadowing of the 3D spider. Therefore, we predicted that bees should have a higher probability of being attacked by cryptic spiders and would therefore display slower avoidance learning in comparison with bees encountering highly conspicuous spiders. We tested this hypothesis by using a seminatural predator-avoidance paradigm in which bees foraging in a flight arena containing artificial flowers were exposed to controlled predation threat from remotely controlled electromechanical spider models (henceforth “spiders”) that differed in conspicuousness. Bees received a simulated predation attempt whenever they landed and attempted to feed on a flower harboring a spider (Figure 1). Spiders were present on 4 out of 16 flowers, so random flower choice would have resulted in a 25% chance of being attacked.

Probability of Being Captured: A Speed-Accuracy Tradeoff?

We expected bees encountering cryptic spiders to make more mistakes (landing on flowers with spiders) because they should make more detection errors. Although there was a trend for bees in the cryptic-spider treatment to make more errors than bees in the conspicuous-spider treatment, the trend was not significant during either training or later memory tests (Figure 2). On average, bees received seven simulated predation attempts (in which they were captured and held for 2 s [Figure 1]) during the first 200 visits of the training stage, irrespective of spider conspicuousness (conspicuous = 7.0 ± 0.7 attacks; cryptic = 7.1 ± 0.6 attacks: $F_{1,30} = 0.018$, $p = 0.896$).

Initial spider-encounter rates (Figure 2A, first 25 visits) were close to random (0.25) for all bees, indicating a lack of an innate response to the visual appearance of the spiders (but see [10, 13]). However, as soon as bees started to receive predation attempts, the rate of erroneous visits to dangerous flowers fell exponentially (Figure 2B). Surprisingly, the probability of attack fell at the same rate for bees encountering cryptic or conspicuous spiders (slope coefficient of the learning curves in Figure 2B: $F_{1,26} = 0.01$, $p = 0.921$). However, by using 3D video tracking software, we identified a potential speed-accuracy tradeoff [7], previously unknown in the context of predator avoidance.

Bees responded to the presence of cryptic spiders by slowing down their inspection flights relative to bees encountering conspicuous spiders (Figure 3). Throughout training, bees encountering cryptic spiders consistently spent longer inspecting and rejecting dangerous flowers than bees encountering conspicuous spiders (Figure 3A: repeated-measures ANOVA: $F_{7,175} = 2.26$, $p = 0.031$). This difference was more marked toward the end of the training phase, suggesting that bees became increasingly cautious as they learned that the meadow contained cryptic predators (Figure 3A). Furthermore, the disparity in inspection times of dangerous flowers continued into the midterm-memory test (16.3 ± 0.8 min after training) and the overnight-retention test (23.4 ± 0.3 hr later), in which bees had to choose between safe and dangerous flowers but were not trapped by the robotic spiders (Figure 3B). Bees encountering cryptic spiders were as accurate at avoiding flowers with spiders as bees encountering conspicuous

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Figure 1. Schematic View of a Simulated Predation Attempt

(A) shows a plan view of the solenoid-powered trapping mechanism (not to scale). As a bee lands to feed, the robotic spider (spider model and trapping mechanism) is activated, causing the trap pads to close rapidly (B) and trap the bee for 2 s (C). Drawings by Sara Blackburn.

spiders, but they took nearly 1.7 times longer inspecting and rejecting these flowers in the midterm-memory test (Figure 3B: $F_{1,28} = 20.57$, $p < 0.001$) and 1.4 times longer in the overnight-retention test (Figure 3B: $F_{1,28} = 9.78$, $p = 0.004$).

These differences indicate that bees encountering cryptic spiders maintained their accuracy at rejecting flowers harboring spiders by spending longer inspecting the flowers. This speed-accuracy tradeoff is all the more interesting because it appears to be selective: Bees do not alter their flight behavior when they have learned that spiders are easy to detect.

False Alarms

A common assumption about memory is that learned associations and responses tend to fade over time without further reinforcement [14–17]. However, memory can be highly durable in insects [18–20], and in some animals, memories (or responses to past events) can actually intensify over time despite the absence of new learning trials [21]. Indeed, we found that the learned predator-avoidance response of bumblebees subjected to simulated predation attempts at flowers harboring either conspicuous or cryptic spiders was persistent over at least 24 hr

(Figures 2C and 2D). More importantly, we identified an important relationship between predator conspicuousness and the frequency of “false alarms” (i.e., erroneous rejection of flowers without predators), a relationship that indicated that subjective perception of risk actually increased after overnight memory consolidation.

Avoidance of dangerous flowers did not change significantly between the end of training and the midterm-memory test (Figure 2C; conspicuous: $t = 1.95$, $p = 0.070$, $df = 15$; cryptic: $t = 0.49$, $p < 0.629$, $df = 14$), although there was a trend for increased avoidance when conspicuous spiders were present. Predator avoidance of bees encountering either conspicuous or cryptic spiders was also remarkably well maintained between the reinforcement training and the overnight-retention test 23.4 ± 0.3 hr later (Figure 2D; conspicuous: $t = 0.51$, $p < 0.619$, $df = 14$; cryptic: $t = 1.24$, $p = 0.237$, $df = 14$). However, during this test, bees encountering cryptic spiders rejected significantly more flowers (Figure 4A without spiders, Mann-Whitney $U = 43.5$, $p = 0.013$ and Figure 4B with spiders: $U = 53.5$, $p = 0.042$). The increased rate of false alarms indicates that bees are extending their perception of danger to all yellow flowers rather than just those with cryptic spiders. Such generalized overcautiousness could explain why bees sometimes altogether avoid patches of flowers harboring high densities

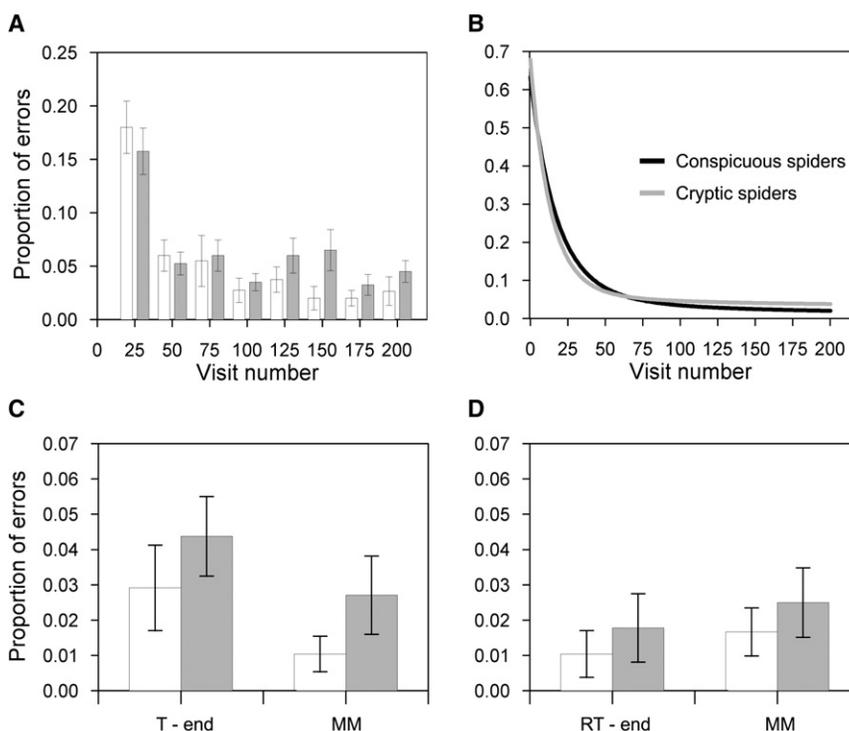


Figure 2. Accuracy of Avoidance Learning and Memory

(A) Average learning performance during the training stage. Each bar represents the mean (± 1 SEM) proportion of errors made by bees (conspicuous-spider treatment: $n = 15$, cryptic-spider treatment: $n = 16$) during consecutive blocks of 25 flower visits. White bars represent bees encountering cryptic spiders, and gray bars represent bees encountering conspicuous spiders.

(B) Learning curves showing the mean predicted error rates calculated from individual curve fits for bees in each treatment.

(C and D) (C) shows the change in performance between the end of training (T - end) and the midterm-memory (MM) test (average time interval of 16.3 ± 0.8 min), and (D) shows the change between reinforcement training (RT - end) and the overnight-retention (OR) test (average time interval of 23.4 ± 0.3 hr). The conspicuous-spider group is shown by white bars, and the cryptic group is shown by gray bars. Error bars represent ± 1 SEM.

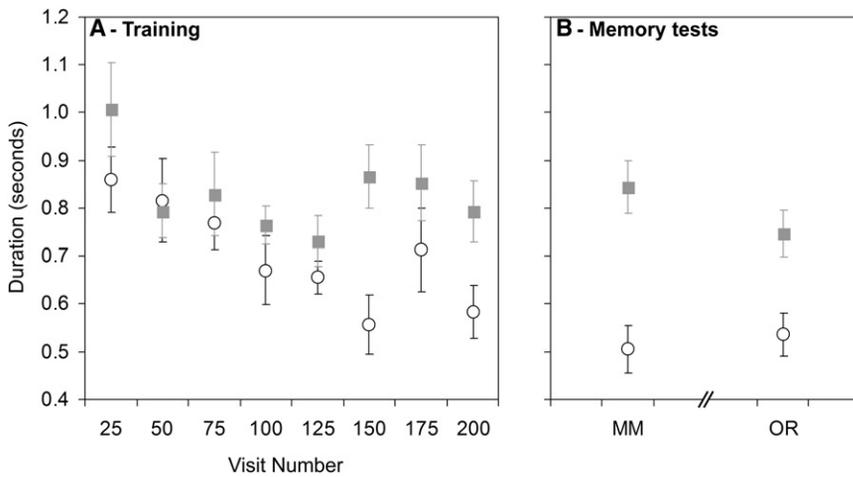


Figure 3. Speed of Rejection of Dangerous Flowers by Bees Encountering Robotic Spiders. In both panels, white circles are used for conspicuous spiders, and gray squares are used for cryptic spiders.

(A) Changes in mean (± 1 SEM) inspection-flight durations during the training stage: For every 25 flower visits, each data point represents treatment means of the average time individual bees spent inspecting and rejecting dangerous flowers during the period when the 25 visits were made. Bees in the cryptic-spider group spent significantly longer inspecting flowers than bees in the conspicuous-spider group (repeated-measures ANOVA, spider-visit interaction: $F_{7,175} = 2.26$, $p = 0.031$).

(B) Inspection-flight duration (mean ± 1 SEM) for dangerous flowers rejected by bees encountering conspicuous (white circles) or cryptic (gray squares) spiders during the midterm-memory test (MM, conspicuous $n = 15$ and cryptic $n = 15$ bees) and the overnight-retention test (OR, conspicuous $n = 13$ and cryptic $n = 15$ bees).

of crab spiders [22–24]. Indeed, we also observed that seven out of ten bees that left the flower patch altogether after three to four predation attempts had been encountering cryptic spiders.

Conclusions

Predator-avoidance learning is not static, and bumblebees show considerable behavioral flexibility when exposed to predation threat. The two main results of this study indicate that bees are able to compensate for the presence of cryptic predators and maintain high levels of predator detection. However, this leveling of risk comes with the cost of increased flower-scanning times and false alarms. Therefore, bees encountering cryptic predators trade off reduced foraging efficiency for increased safety from predation. These findings could have important implications for the evolution of crypsis in predators and plant fitness and community structure [25, 26]. From a predator’s perspective, any advantages gained by better crypsis could potentially be undone by more cautious behavior of prey, forcing predators to adjust their strategy further. Prey, conversely, might abandon foraging patches not directly because of predation risk, but because the costs of detecting predators might ultimately make the patch less valuable. In the case of the triangular interaction between pollinators, plants, and floral ambush predators, plants might suffer fitness costs from predator infestation [26, 27] because any investment the plant makes to increase flower detectability might be offset by pollinators having to invest extra time to examine floral displays for the presence of predators. These considerations show that the ecology of predator-prey interactions could draw substantial benefit from borrowing psychological concepts of visual search and signal-detection theory.

Experimental Procedures

Predator-Avoidance Learning Paradigm

Nectar-foraging bumblebees (*Bombus terrestris dalmaninus* Dalla Torre) were presented with an “artificial meadow” (hereafter “meadow”) containing a mixture of “safe” and “dangerous” flowers. Bees were offered food rewards at all flowers but also received a simulated predation attempt by a crab spider when they attempted to feed on dangerous flowers. The meadow, consisting of 16 artificial flowers arranged in a 4×4 vertical grid on a gray background (painted gray with Dulux Eggshell 00NN31000CN8), was housed in a wooden flight arena ($l = 1$ m, $w = 0.72$ m, and $h = 0.73$ m;

other walls painted white with Crown Kitchen & Bathroom, Pure Brilliant White Matt) covered with a clear UV-transmittent Plexiglas lid. Each flower consisted of a detachable yellow floral signal (7×7 cm square [1 mm thick] acrylic, painted with Plasti-kote Satin Super, 2104 Daffodil) and an artificial feeder. Bees accessed food at the feeders through a hole in the arena wall, 10 mm above a wooden landing platform (40×60 mm) flanked by two trap pads ($35 \times 10 \times 20$ mm wooden blocks with their inside surface coated in $35 \times 10 \times 20$ mm white foam; Figure 1). All wooden parts were painted with the same gray paint as the wall.

A constant flow (1.85 ± 0.3 μ l per minute) of food (50% [v/v] sucrose solution: hereafter “nectar”) was supplied to each flower using syringe pumps (KD Scientific, KD200, Holliston, USA). Droplets of nectar formed at the tip of syringe needles (BD Microlance, Drogheda, Ireland, 3 26G 0.45 \times 13 mm) and were accessible to bees through holes in the meadow wall above the landing platforms. Droplets reached a volume of 4.70 ± 0.3 μ l before falling into a waste pot (not accessible to bees) and being replenished (Figure S2). This simulated a patch where flowers were regularly emptied by other bees and thus prevented unvisited flowers from becoming substantially more rewarding than visited flowers.

Robotic spiders were used to simulate predation attempts at dangerous flowers. Each robotic spider consisted of an active trapping mechanism (see below) and a life-size crab spider (*Misumena vatia*) model ($l = 12$ mm, made from Gedeo Crystal Resin) placed on the floral signal above the feeding hole (Figure 1). The custom-built trapping mechanisms (Liversidge & Atkinson, Romford, UK), housed on shelving behind the meadow wall, were powered by remotely controlled solenoids (TU.1939P 24V DC, H. Kuhnke Ltd, Romsey, UK) that rapidly closed two caliper-hinged arms (Figure 1). The arms of the traps protruded through the meadow wall, ending in padded jaws (see above) that could capture and hold a bee for a controlled duration (2 s in this study) without causing physical damage (all trapped bees continued foraging after the experiments).

Experimental Conditions

Two small colonies (with 20–30 workers) of bumblebees (*B. terrestris*) were obtained from a commercial supplier (Syngenta Bioline Bees, Weert, Netherlands). Bees were kept under a 12 hr light/dark cycle (light: 08:00 to 20:00) throughout the experiments, with controlled illumination provided by high-frequency fluorescent lighting (TMS 24F lamps with HF-B 236 TLD [4.3 KHz] ballasts, Philips, Eindhoven, Netherlands, fitted with Activa daylight fluorescent tubes, Osram, München, Germany) emitting light with a flicker (4.3 KHz) well above the flicker-fusion frequency of bees [12] and mimicking natural daylight, including a near-ultraviolet component.

Predator-Visibility Treatments

Two groups of bees (equally split across two colonies) were tested under two predator-avoidance paradigms in which dangerous flowers harbored either highly conspicuous spiders (white model on yellow flower) or cryptic spiders (yellow model on yellow flower). In both treatments, 4 out of the 16 flowers were randomly designated as dangerous flowers, i.e., they harbored robotic spiders that trapped bees for two seconds as they attempted to

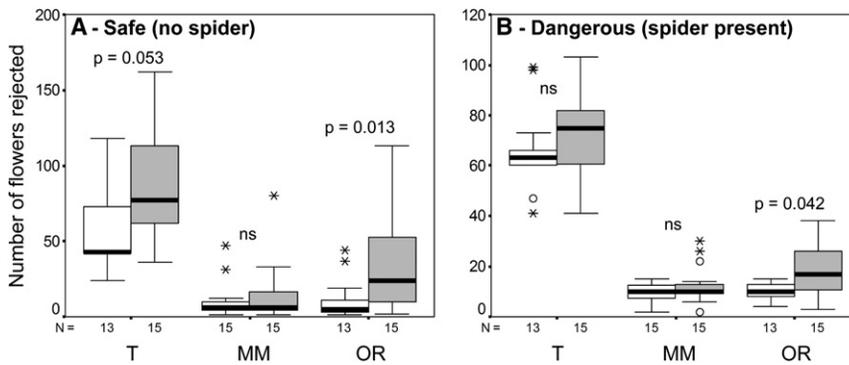


Figure 4. The Number of Flowers Rejected by Bees Encountering Robotic Spiders

(A) shows false alarms (flowers without spiders), and (B) shows true alarms (dangerous flowers with spiders). White boxes represent the conspicuous-spider treatment, and gray boxes represent the cryptic-spider treatment. Horizontal axis labels correspond to different experimental stages: training (T), the midterm-memory test (MM), and the overnight-retention test (OR). For each box, solid black bars are median values, and the upper and lower edges are the 75% and 25% quartiles, respectively. The whiskers show maximum and minimum values that are not outliers (open circles) or extreme values (asterisks). The numbers along the horizontal axis are the numbers of bees in each treatment. P values correspond to Mann-Whitney tests comparing spider visibility treatments during each stage (ns = nonsignificant).

feed. Thus, random visitation would yield an attack frequency of 25%. Conspicuous white spiders (painted with Plasti-kote Satin Super, 2101/Ral 9010 White) were highly distinguishable from the yellow flowers in bee color space (Figure S1). In contrast, cryptic spiders were painted the same yellow color as the flowers and were therefore virtually indistinguishable from the flowers in terms of color alone (Figure S1). Despite this inconspicuousness, bees could of course infer shape cues from shading by hovering closely in front of the flowers.

Learning and Memory Tests

The food supply within colonies was checked prior to testing, and to eliminate potentially confounding effects of nutritional status on risk aversiveness [28], 2 ml of 50% (v/v) sucrose solution was added to the colony if it contained fewer than three full honey pots. Furthermore, before testing began, all bees were given free access to the flight arena and allowed to forage from the feeders without floral signals (i.e., a neutral gray background). Motivated foragers were identified (they filled their crops and returned to the nest [a foraging bout] at least five times), and a single forager was selected for testing. When the selected bee returned to the nest, all other bees were removed from the flight arena.

The learning and memory tests for both groups of bees were subdivided into seven distinct stages:

Stage 1 – Pretraining

During this stage, individual bees foraged in the meadow containing 16 safe yellow flowers for a minimum of 100 flower visits (bees landed on the landing platforms and either fed or rejected the flower) to ensure they had learned to associate yellow flowers with nectar rewards (bees were already experienced at using the feeders without yellow floral signals). To avoid undue disturbance during the tests, bees were allowed to finish the foraging bout in which they reached the minimum number of visits in each stage.

Stage 2 – Training

Four randomly selected flowers in the meadow “became dangerous” (they harbored robotic spiders). Bees were allowed to forage until they landed on at least 200 flowers (20 to 30 min foraging time). They were trapped by the robotic spiders for 2 s whenever they landed and attempted to feed on a dangerous flower. The positions of the dangerous flowers were randomized between foraging bouts.

Stage 3 – Neutral

All yellow flower signals were removed, and bees were allowed to forage on the neutral feeders for at least 50 flower visits. This stage was included to provide a break between training and the memory test while ensuring that bees remained motivated foragers.

Stage 4 – Midterm-Memory Test

Immediately after the neutral phase (16.3 ± 0.8 min after the end of training), the 12 safe and 4 dangerous flowers were returned to the meadow in a newly randomized pattern. Bees were allowed to forage for a minimum of 30 visits (4 to 6 min foraging time) and were not trapped if they visited dangerous flowers.

Stage 5 – Reinforcement Training

This stage was necessary because bees might have learned about the absence of predation threat during the previous memory test. Reinforcement training was essentially a shorter (minimum of 50 visits) repeat of stage 2.

After this stage, the bees were allowed to forage again on landing platforms without any floral signals.

Stage 6 – Remotivation

On the next day, bees were prepared for the overnight-retention test. The bees were allowed to forage alone in the meadow on the feeders without floral signals up to a minimum of 50 flower visits so that they remained motivated nectar foragers.

Stage 7 – Overnight Retention

Approximately 24 hr (23.4 ± 0.3 hr) after the end of the reinforcement training, bees were presented with a random pattern of 12 safe and 4 dangerous yellow flowers (spiders were present but bees were not captured). They were then allowed to visit at least 30 flowers (4 to 8 min foraging time), after which they were permanently removed from the nest and measured (thorax width).

Data Collection

During the seven stages, the location of all visits was recorded in real time. Visits were scored as either “land and accept” when bees landed and probed the flowers or “land and reject” when bees briefly landed without attempting to probe the flowers. The flight behavior of bees was recorded during all stages. Three-dimensional positions of bees were calculated 50 times per second with two video cameras connected to a computer running Trackit 3D software (BIOBSERVE GmbH, Bonn, Germany).

Data Analysis

A total of 42 bees were pretrained to visit yellow flowers. During training, 10 bees ceased foraging before the minimum criterion of 200 visits was met (they visited an average of 51.2 ± 17.1 flowers and were trapped 3.6 ± 0.5 times). Individual predator-avoidance learning curves were fitted to the flower visits made by the remaining 32 bees during the training stage with a first-order exponential decay function ($y = y_0 + Ae^{-x/t}$) in Microcal Origin [29, 30]. Visits to safe flowers were scored as correct and visits to dangerous flowers were scored as incorrect. The 200 flower visits of the stage were subdivided into consecutive blocks of 25 visits, allowing the proportion of incorrect choices to be calculated. Learning curves were fitted to these eight proportions, and the slope coefficients t (learning speed) of the curves were used in subsequent analyses. A small number of bees (conspicuous-spider treatment: $n = 2$, cryptic-spider treatment: $n = 1$) did not learn (curve fitting failed or produced extremely poor fits). These bees were excluded from analyses of learning speed.

Comparison of performance between stages was based on the proportion of errors in the last 30 visits of the training and reinforcement stages (to the end of the foraging bout) and the first 30 of the memory-test and overnight-retention stages.

The flight behavior of bees visiting flowers was quantified using the 3D position data to calculate time, distance, and speed of bees as they entered and departed a zone (Figure S3) centered on each individual flower ($d = 7$ cm, $w = 9$ cm, $h = 9$ cm). A smaller feeding zone ($d = 4.5$ cm, $w = 1$ cm, $h = 1$ cm; estimated from average feeding positions), contained within the large zone, was subtracted to exclude time spent feeding from the analysis. Visits to each flower zone were classified as before with the addition of “reject” when bees entered the flower zone but did not land.

Data from the two colonies were pooled because trends did not differ significantly between colonies (Table S1), and the potential effects of bee size and age on learning, memory, and flight parameters were ruled out by correlation analysis (Table S2). Analysis of pooled data was carried out in SPSS for Windows 11.5. Nonparametric tests were used where data (after transformation) did not conform to the assumptions of parametric tests. For flight data, visits of less than 0.1 s were removed so that the chance of including instances of bees passing by a flower without inspecting it would be reduced.

Supplemental Data

Supplemental Data include three figures and two tables and can be found with this article online at <http://www.current-biology.com/cgi/content/full/18/19/1520/DC1/>.

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