

Bumblebees forage on flowers of increasingly complex morphologies despite low success

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Foraging bees expend considerable time and energy handling flowers that are morphologically complex (with concealed food rewards) while simple flowers (with readily available rewards) bloom simultaneously in their foraging environment. Previous studies have investigated the consequences of floral morphology for both foragers and plants, often treating ‘complex’ and ‘simple’ morphologies as dichotomous traits. How pollinators’ foraging choices and success vary along a floral complexity gradient has received less attention. Here we investigated, using real flowers of increasing morphological complexity, how complex flowers are chosen and handled by naïve and experienced bumblebees when presented along with simple ones. Intact flowers of *Tecoma* x ‘Orange Jubilee’ (Bignoniaceae), *Antirrhinum majus* (Plantaginaceae) and *Lupinus pilosus* (Fabaceae) represented a gradient of increasing morphological complexity. We manipulated some flowers of each species to look simple with a readily accessible food reward, while keeping their colour and odour unchanged. *Bombus terrestris* workers were given four simple and four complex flowers of a single species with equal rewards in choice assays in a flight room. Sixty per cent of naïve foragers chose a complex flower on their first visit to all three flower species arrays. Experienced bees visited complex flower types of all three species but had lower feeding success and longer handling times on the more complex species. Thus, the bees’ foraging efficiency on the complex option decreased with increasing complexity of the flowers, while individual variation in feeding success on the complex option was increased. These results suggest that inexperienced foragers and unsuccessful feeding attempts increasingly contribute to floral pollination along the morphological complexity gradient.

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Shape as a floral signal influences the process of pollination, as it functions as an attractive trait and confers structural features that affect the mechanical/physical fit between flowers and their pollinators (Gómez, Perfectti, & Camacho, 2006; Thomson & Stratton, 1985). Flower shapes vary in morphological complexity. Structurally simple flowers are those with nectar and pollen rewards easily accessible to their pollinators. Complex (also termed specialized) flowers, on the other hand, typically possess features that restrict the access to nectar and pollen rewards, such as long narrow tubes and blocked entrances (Neal, Dafni, & Giurfa, 1998; more examples in Krishna & Keasar, 2018). Such complex structures have been proposed to increase floral constancy and reduce within-plant pollen transfer (geitonogamy), thereby improving pollination

efficiency and plant fitness (Ohashi, 2002; Santamaría & Rodríguez-Gironés, 2007; Stout, Allen, & Goulson, 1998).

To coexist with plants that have simple flowers, species with complex floral morphologies must attract enough pollinator visits. Although there have been few large-scale studies of the relationship between complexity and reward properties, theoretical predictions and empirical data suggest this relationship is positive (Cohen & Shmida, 1993; Peleg, Shmida, & Ellner, 1992; Petanidou & Smets, 1995; Potts et al., 2003). Generalist pollinators such as bees gain from reduced competition at complex flowers, and so possibly collect higher rewards. However, they need to persevere and learn the reward extraction routines to become adept at handling these flowers (Borrell, 2005; Gegeer & Laverty, 1995; Peleg et al., 1992; Stang, Klinkhamer, & Van Der Meijden, 2006). From an optimal foraging theory perspective, learning to handle complex flowers is energetically expensive at the outset, requiring much longer time while providing minimal rewards. Simple operant learning, which involves repeated performance of highly rewarding motor sequences, does not explain such persistence on complex tasks

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despite the availability of simpler alternatives. The potential role of other choice mechanisms in the learning of complex flowers is intriguing.

The ubiquity of large rewards in complex flowers may favour a coevolutionary response by pollinators, resulting in innate predispositions towards complex features. Muth, Keasar, and Dornhaus (2015) addressed this hypothesis but did not find any innate preferences for complex artificial flowers. Preference for complex flowers developed gradually only when these flowers offered higher food rewards than simple ones, and were purple, a colour favoured by the bees. In the present study we expanded Muth et al.'s (2015) work in two ways. First, we documented the choices of bumblebees that were presented with natural complex and simple flowers, rather than with artificial flower-like feeders. Similar manipulations of natural flowers have been used in previous foraging experiments with bees (Russell, Mauerman, Golden, & Papaj, 2018). Second, we tested the bees' responses to three flower species of increasing complexity, while Muth et al. (2015) studied a single complex morphology.

Each bee in the present study foraged on equally rewarding flowers of one of the three species, half of them experimentally simplified and the rest with unaltered morphology. This generated three levels of handling difficulty for the complex foraging option, while the simplified flowers (the simple option) required similar handling effort in all species. We specifically asked the following questions, concerning this increasing difference in handling difficulty between the two feeding options. (1) Are the initial choices of flower-naïve bees affected by the difficulty level of the complex option? Based on previous evidence for indifference to complexity by naïve bees (Muth et al., 2015), we expected the answer to be negative. (2) Are the floral preferences of experienced bees affected by the difficulty level of the complex option? In some field studies, plant species with specialized flowers received as many pollinator visits as species with simple flowers (Hegland & Totland, 2005; Ohashi, 2002). In other investigations with real (Lázaro, Jakobsson, & Totland, 2013; McCall & Primack, 1992) and artificial (Muth et al., 2015; Saleh, Ohashi, Thomson, & Chittka, 2006) flowers, experienced foragers preferred simple morphologies to complex ones. We hypothesized that these contrasting findings are due to differences in the handling difficulty of the specialized flowers, namely, that experienced foragers only discriminate against complex flowers that they cannot handle quickly and effectively after practice. Thus, we predicted fewer choices of the complex foraging option as it becomes increasingly hard to learn. (3) Does the individual variation among bees visiting complex versus simple flowers increase as the complex option gradually becomes more difficult to handle? We predicted that most individuals would visit both the simple and the complex morphologies when they do not differ greatly in handling technique. As the difference between the two flower types increases, individual foraging specializations may emerge. In particular, we predicted that, with increasing handling difficulty, fewer bees would feed on both flower types, while more foragers will specialize on one of the flower morphologies. We examined individual body size, reward specialization tendencies and age of the colony, which may be associated with foraging specializations along the floral complexity gradient.

METHODS

Colonies of *Bombus terrestris* purchased from Polyam, Yad Mordechai, Israel were kept, trained and tested within a 2.90×3.60 m flight room. The room was maintained at 26–29 °C and a relative humidity of 40–60%; it was illuminated by D-65 tube lights between 0600 and 1800 hours. The colony was placed on one side of the room and its entrance was fitted with a small Perspex tunnel

through which the bees came out. Pulverized honeybee-collected pollen was provided directly to the colony in the first week. Afterwards pollen was offered ad libitum in a shallow dish outside the colony after the experimental sessions. Flower-naïve bumblebees were pretrained to feed on scented sucrose solution (concentration 50% w/w), provided in a simple feeder (transparent plastic dish) in the flight room. Bees that learned to forage from the sucrose feeder were individually marked with numbered tags. Bees were provided with nectar and pollen feeders simultaneously outside the colony for 2.5 h, three times a week outside observation sessions. Individual temporary foraging specializations (defined as >85% of the foraging period spent collecting either pollen or nectar) at the feeders were recorded. The dry body mass of foragers was determined after their death. A total of 144 *B. terrestris* workers from five colonies were used in the experiments.

Flowers

Experiments were conducted with three flower species: *Tecoma* × 'Orange Jubilee' (Bignoniaceae, hereafter '*Tecoma*'; $N = 60$ bees from colonies 1 and 2), *Antirrhinum majus* (Plantaginaceae, hereafter '*Antirrhinum*'; $N = 40$ bees from colonies 4 and 5) and *Lupinus pilosus* (Fabaceae, hereafter '*Lupinus*'; $N = 44$ bees from colonies 2, 3 and 4; further details in Appendix Table A1). These flowers scored 2.48, 2.83 and 2.88, respectively, on a floral complexity scale proposed for natural flower communities. The complexity scores of 427 taxa from a Mediterranean plant community ranged from 1.15 to 3.25 according to this scale. The scale is based on the sum of weights assigned to some of the floral features, that is, shape, depth, symmetry, segmentation of the corollas and functional reproductive units that are important for pollination (Stefanaki, Kantsa, Tschulin, Charitonidou, & Petanidou, 2015).

Tecoma and *Antirrhinum* flowers contain nectar as well as pollen while *Lupinus* flowers are nectarless with pollen alone as reward. *Lupinus* flowers comprise a standard banner petal and two lower petals fused into the keel enclosing the reproductive parts. Bees typically hold the lower petals and slide them downwards to access the reward. In *Antirrhinum*, the petals are fused forming a tube with a bilabiate closed mouth and bees force their way inside through the mouth to access the nectar. In *Tecoma*, they just crawl inside the tubular corolla to reach the nectar without pushing open the petals (Fig. 1). Thus, we consider *Tecoma* flowers as having the simplest morphology of the three species, *Antirrhinum* flowers as possessing intermediate complexity and *Lupinus* flowers as the most complex.

Eight freshly clipped flowers of a single species were presented to the bees in all the experiments. The corolla morphology of four flowers was simplified prior to the experiment, while the morphology of the remaining four flowers was left intact (Fig. 1). While simplifying the flowers, we were careful to leave their outline unchanged, so as not to reduce their visibility to foragers. Nectar in the flowers was removed using microcapillary tubes and Whatman filter paper. Anthers were removed to prevent foraging for pollen and any potential scent associated with it. All corollas were pricked with a needle, to control for potential odours emanating from injured tissues during floral manipulations. The prepared flowers were vertically displayed in tubes with florist's foam to prevent desiccation and spaced 10–15 cm apart on the experimental table. Flowers were injected with 1 µl of 30% sucrose solution, as a standard food reward, before they were presented to the bees.

Experimental Design

A single marked worker was allowed to visit four simple and four complex flowers of a single species in each observation

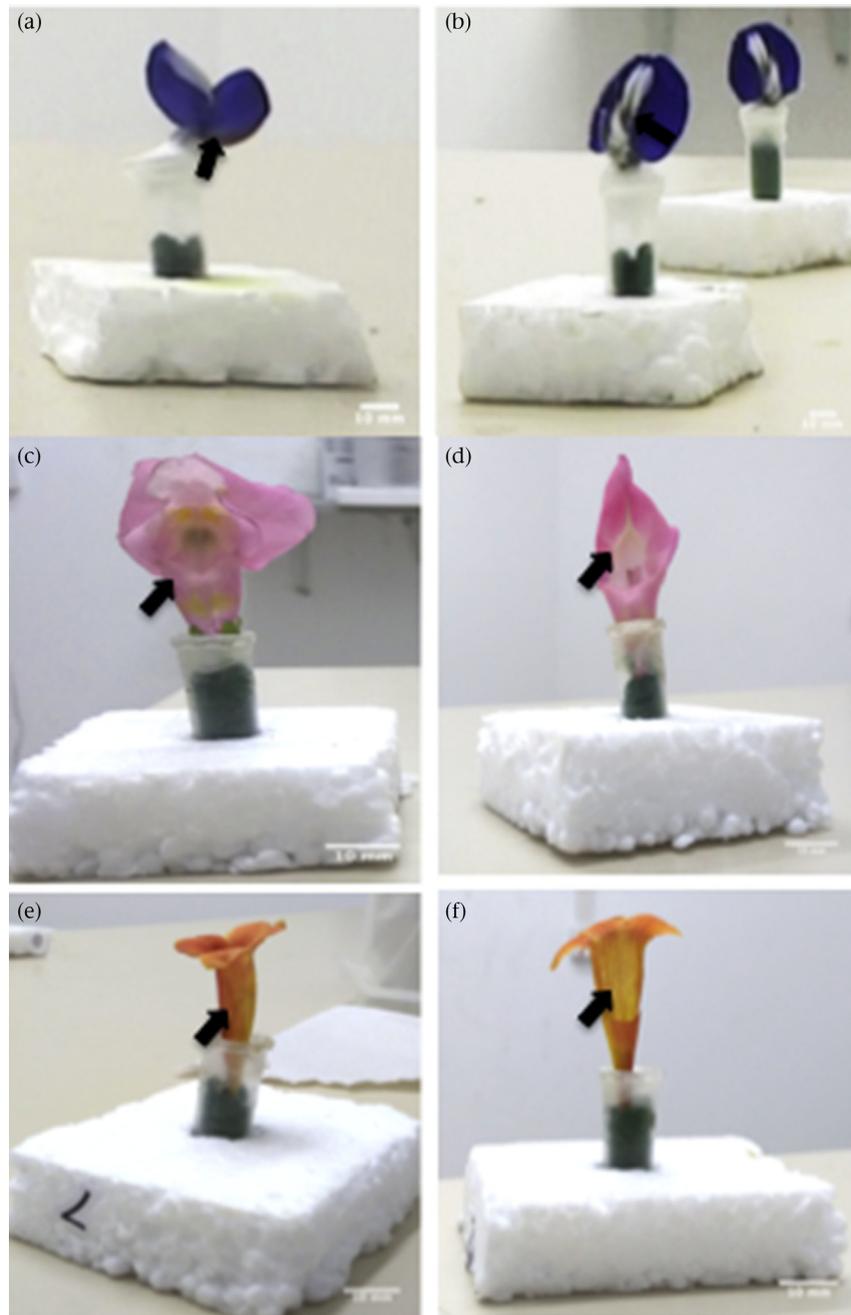


Figure 1. (a, c, e) Complex and (b, d, f) simple (part of the corolla removed) flowers of (a, b) *Lupinus pilosus*, (c, d) *Antirrhinum majus* and (e, f) *Tecoma* x 'Orange Jubilee' with 1 μ l sucrose rewards (reward locations are indicated by black arrows). The flowers were placed in Eppendorf tubes with florist's foam. One bee foraged on four complex and four simple flowers of a single species in each observation session.

session. The bee's behaviour was video recorded until it left the area around the experimental table for >30 min. Each bee was tested on a single day. A typical observation session included three to four foraging bouts (trips from the colony to the flowers and back) over 2 h, with 20–35 flower visits per bout. During the session, immediately after a flower was visited, we replaced it with a fresh flower that had the same morphology at the same location, and that contained 1 μ l sucrose solution reward. Thus, all flowers in the experiment were rewarding throughout the observation session and similar in colour, odour and size, but were either morphologically complex or simple. The location of simple and complex flowers within the array was randomized between

observation sessions. The bees' flower choices and handling times were extracted from the videos manually.

Preliminary Experiment

To test for potential effects of damage to the flower corollas on the bees' responses (Krupnick, Weis, & Campbell, 1999), we ran an experiment with *Tecoma* flowers. In this experiment, the corolla lobes of four flowers were damaged visibly but the tube was left intact to retain their shape and complexity (Fig. A1). The area of the flower tissue clipped was comparable to the area removed to make flowers simpler in the main experiment. These flowers were

presented to the bees together with four intact flowers, using the same general design as in the main experiment described above. The initial choices and percentage visits to the two flower types were compared ($N = 10$ bees from colony 6, [Table A2](#)). Fifty per cent of the bees landed on a damaged flower on their first visit. Moreover, the overall mean proportions of visits to damaged (0.53) and intact (0.47) complex flowers did not differ significantly (Wilcoxon paired test: $V = 39$, $P = 0.27$).

Ethical Note

Bees used in the experiments were housed at appropriate temperature and humidity conditions. They received sugar solution and pollen every day. Bees were captured for marking while they were feeding, using plastic cages with sponge plungers. Colonies were frozen only after natural death of all individuals. No approval of the animal ethics committee was needed because the research subjects were invertebrates.

Data analysis

We pooled data across the colonies for each flower species array, since there were no significant differences in choices between them (*Tecoma*: $X^2_1 = 0.04$, $P = 0.83$; *Antirrhinum*: $X^2_1 = 3.68$, $P = 0.05$; *Lupinus*: $X^2_1 = 2.20$, $P = 0.33$). Of the tested bees, 72 made fewer than 35 visits ([Table A1](#)). Data from these individuals were only included in the analyses pertaining to first choices and overall preferences. All data were analysed using R version 3.5.0 ([R Development Core Team, 2016](#)). [Table A3](#) provides an overview of the statistical tests performed.

Behaviour Coding

We defined bees in the videos as having visited a flower if their legs contacted it and we used the proportion of landings on the two flower types as a measure of preference. If a bee located the reward in a flower and extended its proboscis to feed on it, we recorded this as a successful visit. Handling time was defined as the interval between landing on a flower and the end of feeding. For visits that did not result in feeding, we measured the total time spent on the flower rather than handling time.

Innate and Overall Preferences

Binomial tests were used to analyse whether bees preferred simple or complex flowers in their first landing choice (irrespective of the visit being successful or not) as well as in their overall choices.

Effects of Experience

To analyse the effect of experience on handling time, we ran a linear mixed-effects model (LMM; [Bates, Mächler, Bolker, & Walker, 2015](#)). This model tested whether handling time was influenced by the bees' experience, flower species and flower type (complex or simple). Handling times decreased with experience and generally stabilized within 30–40 visits (see Results section below). We therefore considered the first 35 visits as early visits by inexperienced foragers and visits after 35 as performed by experienced foragers. To test for effects of experience (two levels, <35 visits and after 35 visits) on percentage choices of complex flowers, we ran two LMMs, one with percentage successful visits to complex flowers and the other with all visits to complex flowers as response variables. See the Appendix for additional details on the models.

Individual Variation and Its Potential Sources

To determine the extent of variation in individual choices within and between species, we calculated a repeatability measure (R ,

ratio of between-species and within-species variance) and tested its significance by likelihood ratio tests ([Stoffel, Nakagawa, & Schielzeth, 2017](#)). An R value of 0 indicates high variance among individuals that visited the same flower species and 1 indicates low within-species variance and high variance between foragers that were tested on different flower species. We used Spearman correlation tests to examine the relationships between several features of the individuals' early foraging experience and their choices (details in the Appendix).

Colony Age, Forager Size and Pollen/Nectar Specialization. To test for additional possible sources of variability among foragers, we ran a linear model with the percentage of overall visits to complex flowers (log transformed) by individual foragers as a response variable. The data from each flower species were analysed separately, to detect any species-specific predictors of foraging choices. Colony age during testing, foraging specialization (nectar/pollen) and body mass were considered as independent variables. Colony age was used as a categorical variable with three levels: early (1–15 days following procurement), growth (days 16–30) and late stages (day 31 onwards). As the percentage successful visits to complex flowers did not satisfy the assumptions of a linear model, we used nonparametric tests for the individual variables (correlation tests for body mass and Kruskal–Wallis tests for colony age and foraging specialization).

RESULTS

Innate Preferences

The number of flower-naïve bees that made their first landing on a complex flower type was significantly higher than the random expectation ($N = 144$, binomial test: $P = 0.007$). When individual flower species' arrays were considered, most of the bees made their first landings on complex flowers (*Tecoma*: 61.6% of the bees; *Antirrhinum*: 60%; *Lupinus*: 59%). However, first choices of complex flowers were significantly more common than random only for bees tested on *Tecoma* (binomial tests: *Tecoma*: $P = 0.046$; *Antirrhinum*: $P = 0.134$; *Lupinus*: $P = 0.145$). Of the 87 bees that made their first landings on complex flowers, 37 were unsuccessful at accessing the reward at this first attempt. The proportion of bees that were unsuccessful on their first visit increased with floral complexity (*Tecoma*: 0.13; *Antirrhinum*: 0.41; *Lupinus*: 0.69).

Effects of Experience

Handling times of simple and complex flowers

The handling time required to access rewards in both the flower types declined with experience (LMM: $X^2_{15} = 8968.2$, $P < 0.001$; for post hoc comparisons see [Table A4](#) and for variability among colonies see [Table A5](#)) and varied significantly between species (post hoc Tukey's test: $P < 0.001$ for all species pairs). Handling time on complex flowers decreased substantially after 35 visits in all three species (mean reductions in handling times: *Tecoma*: 55.65%; *Antirrhinum*: 35.09%; *Lupinus*: 57.95%). Nevertheless, experienced foragers still spent more time accessing rewards from complex flowers than from the simple ones (Wilcoxon paired tests: *Tecoma*: $W = 510.5$, $P < 0.001$; *Antirrhinum*: $W = 320$, $P < 0.001$; *Lupinus*: $W = 154.5$, $P < 0.001$). Handling times of simple flowers stabilized at 4–5 s after about 30 visits in all three species. Handling times of complex flowers stabilized after 40 visits in *Tecoma* (mean \pm SE: 5.10 ± 0.26 s) and *Antirrhinum* (7.9 ± 0.39 s) and only after 50 visits in *Lupinus* (11.83 ± 2.79 s). Thus, the simplified flowers of all three species were similar in handling difficulty, but learning to handle

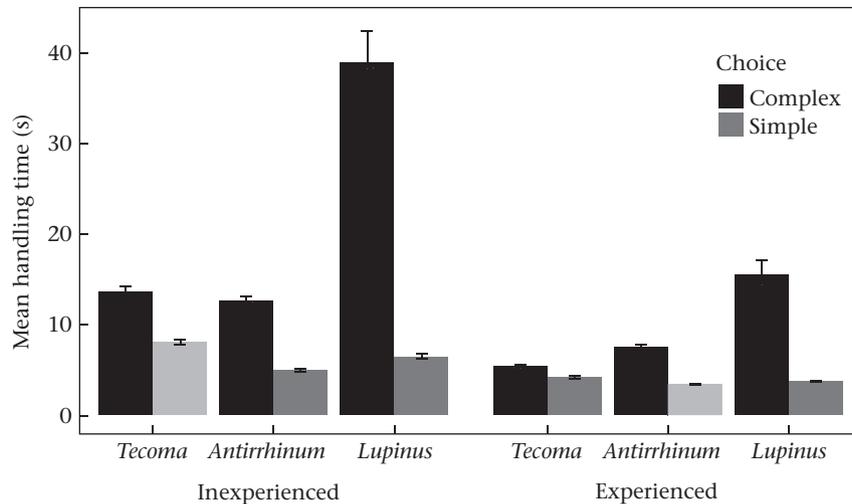


Figure 2. Mean (\pm SE) handling time for visits made to complex and simple flowers in *Tecoma*, *Antirrhinum* and *Lupinus* arrays by inexperienced (< 35 visits) and experienced (> 35 visits) bees.

the intact flowers of *Tecoma*, *Antirrhinum* and *Lupinus* was increasingly difficult for the bees (Fig. 2).

Foragers' preferences for simple and complex flowers

All visits. Bees persistently visited complex flowers in all three species tested (Fig. 3). The mean \pm SE percentages of visits to complex flowers were $54.0 \pm 1.51\%$ in *Tecoma*, $48.9 \pm 3.77\%$ in *Antirrhinum* and $43.7 \pm 2.38\%$ in *Lupinus*. In *Tecoma*, the overall landings were significantly more common on complex flowers than on simple ones ($N = 60$, binomial test: $P = 0.002$). The numbers of landings on the two flower types were similar in *Antirrhinum* ($N = 40$, $P = 0.83$) and *Lupinus* ($N = 44$, $P = 0.99$). The percentage visits to complex flowers declined with experience and varied between species (LMM: $X^2_3 = 20.21$, $P < 0.001$). Tukey's post hoc comparison showed that the percentage visits varied significantly between *Tecoma* and *Lupinus* ($P < 0.001$), but not between either of these species and *Antirrhinum*. Of the 72 individuals that completed

more than 35 visits, specializations on both flower types were equally common: 14 bees specialized on complex flowers, 17 bees on simple flowers and 41 bees landed on both flower types at similar frequencies. We arbitrarily defined individual foraging specialization as more than 60% of the visits directed to one of the flower types, and tested whether foragers specialized on simple flowers after their first 35 visits. The mean frequency of visits to simple flowers by experienced bees did not exceed 60% in any of the species (one-sample t tests: *Tecoma*: $t_{26} = -5.27$, $P = 1$; *Antirrhinum*: $t_{18} = -1.68$, $P = 0.94$; *Lupinus*: $t_{18} = 1.66$, $P = 0.05$).

To understand the variation in foraging patterns in different flower species' arrays, we calculated mean run lengths (consecutive visits to a flower type) of bees. Run lengths to simple flowers increased, while those to complex flowers decreased significantly between naïve and experienced foragers in *Lupinus* arrays (Wilcoxon paired test: $V = 282.5$, $P = 0.001$). No such differences were seen in the other two species' arrays (Fig. 4). Despite the high

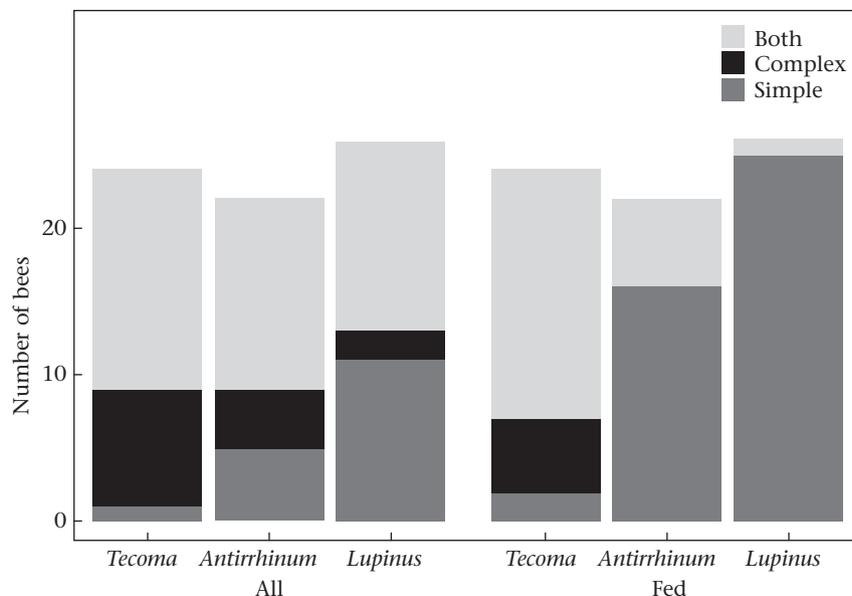


Figure 3. Numbers of bees that visited (All) and that successfully accessed the reward (Fed) from both simple and complex flowers at similar frequencies, and those that specialized ($> 60\%$ of visits) on complex or simple flowers in *Tecoma*, *Antirrhinum* and *Lupinus* arrays.

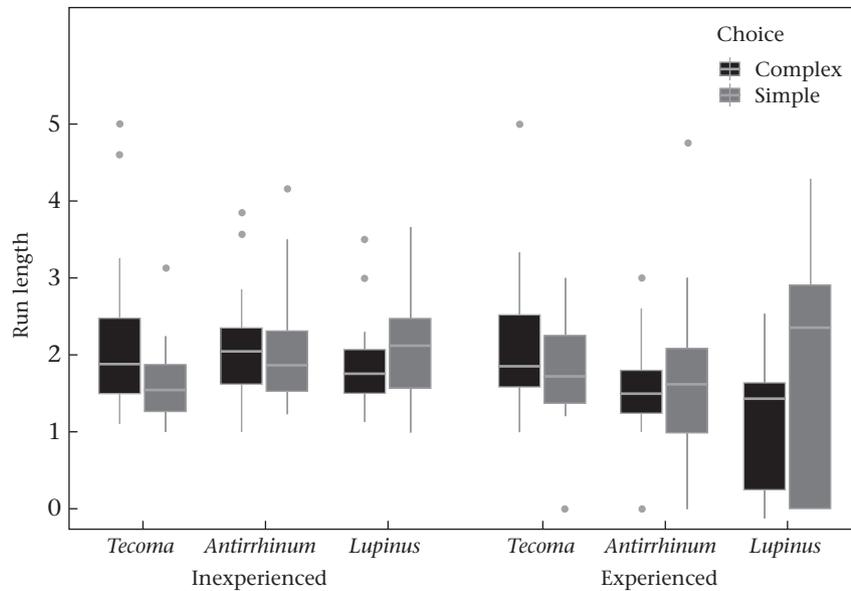


Figure 4. Mean run lengths (consecutive visits to a flower type) on complex and simple flowers by inexperienced (first 35 visits) and experienced (> 35 visits) bees in *Tecoma*, *Antirrhinum* and *Lupinus* arrays. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

variation between individuals, this decrease in run length can partly explain the reduced visits to complex *Lupinus* flowers by experienced bees.

Successful visits. Of the 72 foragers that completed more than 35 visits, five specialized in feeding (i.e. directed > 60% of successful visits) from complex flowers, 43 specialized on simple flowers while 24 bees fed from both the flower types. When the degree of complexity increased, the number of bees that specialized on simpler flower types also increased (Fig. 3). The percentage of successful visits to complex flowers varied with species (LMM: $X^2_3 = 111.32$, $P < 0.001$) but not with experience. Tukey's post hoc comparison suggests that percentages of successful visits to complex flowers were higher in *Tecoma* and *Antirrhinum* than in *Lupinus* ($P < 0.001$). Thus, in *Lupinus* alone, experienced bees accessed the reward largely (>60%) from simple flowers (one-sample t tests: *Tecoma*: $t_{23} = -3.22$, $P = 0.99$; *Antirrhinum*: $t_{17} = 0.45$, $P = 0.32$; *Lupinus*: $t_{17} = 22.45$, $P < 0.001$). Of the visits to complex *Lupinus* flowers 79% involved unsuccessful probing attempts that did not lead to sucrose feeding. The frequencies of similar unsuccessful attempts were considerably lower in *Antirrhinum* (9%) and *Tecoma* (2.1%). To identify possible predictors of these unsuccessful attempts in *Lupinus*, we characterized the two visits that preceded them in each bee's visit sequence. Unsuccessful visits to complex *Lupinus* flowers were often preceded by two successful visits to simple flowers (mean proportion: 0.21), two unsuccessful visits to complex flowers (0.20), or one unsuccessful complex visit followed by a successful simple flower visit (0.15). The remaining combinations were considerably less frequent (< 0.10). Thus, recent success on simple flowers, or recent failure on complex ones, predicted unsuccessful feeding attempts in complex *Lupinus*.

Individual Variation and Its Potential Sources

The proportion of visits to complex flower types varied among individual bees in all three species (Fig. A2). Much of the total observed variance originated from variation among individuals tested on the same flower species ($R = 0.21$, $P = 0.01$). However,

when the percentage of successful visits was considered (Fig. A2), the variance between bees that foraged on different flower species ($R = 0.68$, $P < 0.001$) was much higher, suggesting the influence of handling difficulty. Variation within species, calculated as the coefficient of variation, was sizably higher in the two relatively complex species (all and successful visits: *Antirrhinum*: 0.36 and 1.19; *Lupinus*: 0.30 and 1.25) compared to *Tecoma* (0.19 and 0.20). We also tested for possible correlations between the different sources of individual variation. Of the tested factors, improvement rate and initial handling time of complex flowers were significantly correlated ($\rho = -0.4$; Table A6).

Early foraging experience

The percentage of successful visits to complex and simple flower types by individual bees increased significantly with their initial success rate on the corresponding flower types (complex flowers: $\rho = 0.69$, $P = 0.001$; simple flowers: $\rho = 0.37$, $P = 0.003$ for the three species combined). Species-wise correlation tests confirmed this result for *Tecoma* and *Lupinus*, but not for *Antirrhinum* (Table A7). Individual initial handling times were not related to their percentage of successful visits ($\rho = 0.11$, $P = 0.43$) and overall visits ($\rho = -0.03$, $P = 0.82$) to complex flowers. Differences in individual preferences were also not related to their rate of improvement in handling flowers during the first 10 visits in *Tecoma* ($\rho = -0.05$, $P = 0.79$), *Antirrhinum* ($\rho = 0.006$, $P = 1$) or *Lupinus* ($\rho = -0.16$, $P = 0.63$) arrays (Table A7).

Colony age, forager size and pollen/nectar specialization

Body mass of the foragers was not correlated with colony age ($\rho = -0.02$, $P = 0.86$); thus, these two variables were considered separately. Colony age during testing, individual body mass and pollen/nectar foraging specialization did not influence individual choices of simple versus complex flowers in the *Tecoma* ($R^2 = 0.07$, $F_{4, 19} = 0.39$, $P = 0.81$) and *Lupinus* ($R^2 = 0.20$, $F_{4, 21} = 1.36$, $P = 0.27$) arrays. However, foragers' tendency to visit complex flowers was influenced by colony age during testing in *Antirrhinum* ($R^2 = 0.53$, $F_{4, 17} = 4.91$, $P = 0.008$), with bees from the growth phase of the colony frequenting the complex flower type ($P < 0.001$; Fig. A2).

Despite similar median percentage choices of bees from the growth and late stages, the large variation in individuals' choices from the late stage could have resulted in the observed statistical significance of the growth stage. None of the tested factors significantly influenced individuals' preferences when successful visits were considered (Table A8).

DISCUSSION

Generalist pollinators such as bumblebees learn to feed from flowers with complex morphologies despite low initial rewards even in the presence of alternatives. In this study, foraging bumblebees encountered increasingly complex flower shapes along with simpler flowers, which offered similar rewards. We found that bumblebees had mild innate preferences for complex flower shapes. We also showed that with increasing complexity of the flowers, bees' foraging efficiency on the complex option decreased while individual variation in feeding success increased. Overall, we suggest that inexperienced foragers and feeding attempts may contribute to floral pollination along the morphological complexity gradient. In other words, even the highly complex flowers are likely to get enough visits for successful pollination either by naïve bees or by bees that make occasional exploratory visits to access the rewards inside.

Contrary to our first prediction, bumblebees showed mild but consistent innate preferences for complex flower shapes in all three species. However, we found that with experience, the initial preference observed for complex flowers declined in species that were difficult to handle. Our results differ from those of Muth et al. (2015), who did not find an innate preference for complex flowers. The dissimilarity between the studies can be attributed to the differences in experimental set-up. Muth et al. (2015) used artificial flowers where different morphologies were marked by different corolla colours. Since colour preferences had a strong effect on the bees' initial choices, they might have masked a weaker effect of morphological complexity. In the current experiment, morphology was not confounded with corolla colour.

Using our preliminary experiment with damaged complex flowers of *Tecoma*, we showed that bees did not perceive the clipped simple flowers as 'damaged'. Avoidance of damaged corollas is therefore unlikely to explain their initial preferences for complex flowers. However, this might not be the case in natural conditions, where flowers and plants attacked by florivores/herbivores were found to be avoided by pollinators, possibly due to reduced rewards and flower numbers (Karban & Strauss, 1993; Krupnick et al., 1999; Krupnick & Weis, 1999).

Bees improved their speed with experience, as seen in previous field and laboratory studies with complex flowers (Gegeer & Laverty, 1998; Laverty, 1980; Muth et al., 2015; Woodward & Laverty, 1992). All the bees learnt to access rewards from complex flowers after a few visits in *Tecoma* and a majority of them did so in the more complex species as well. Apart from innate preferences, the persistence of naïve as well as experienced bees on complex flowers could reflect a cognitive constraint on decision making. Since both flower types had rewards of similar quality and quantity, the time needed to assess the better rewarding flower type might have been sufficiently long to render their discrimination non-profitable. Nevertheless, in line with our second prediction, with increasing complexity, experienced bees preferentially accessed rewards from simple flowers. In particular, bees that gained experience with *Lupinus* fed mostly on the simple flower type, while those that learnt easier tasks (handling *Tecoma* and *Antirrhinum*) fed indiscriminately from both flower types. Thus, once learnt, as seen with *Tecoma* and *Antirrhinum*, complexity does not appear to be an impediment and consequently the cognitive investment

involved in handling apparently changes with experience. Therefore, in field situations, species with moderately complex flowers that bloom together with other species may receive enough visits from pollinators that persevere on them (Stout et al., 1998). However, as the degree of complexity increases, the presence of a simpler option is likely to reduce the ability to persevere in some individuals as seen in our *Lupinus* arrays. Such flowers may receive pollination services through naïve bees' initial visits and from unsuccessful feeding attempts of experienced individuals.

Morphological complexity in flowers is often defined from the perspective of plants. However, the accessibility of the rewards depends entirely on the pollinator group under consideration and on the investment in learning required on their part to reach these hidden rewards. Complexity in flowers and the responses of pollinators to it can be viewed either as a gradient or as discrete structural variations and their requisite handling tactics. In our study, we used a continuous scoring scale, based on morphological criteria such as shape, depth and symmetry (Stefanaki et al., 2015), to compare the complexity of the flower species tested. Consistent with the complexity ranking, the bees' frequency of visiting and feeding frequencies, as well as handling speeds, were highest on intact *Tecoma* flowers and lowest on *Lupinus*. However, the bees' success rates on *Antirrhinum* were only slightly lower than those on *Tecoma* and much higher than those on *Lupinus*, at variance with their complexity scores. This suggests that the complexity scale that we used did not fully capture the handling difficulty of the flowers for bees. Grouping of flowers into discrete classes, based on their handling techniques (e.g. Chittka & Thomson, 1997; Gegeer & Laverty, 1995), may provide an additional useful estimate of their complexity for insect visitors.

Our third prediction, that individual variation among bees increases with the handling difficulty of the complex flowers, is supported by the higher coefficient of variation in the choices of *Lupinus* and *Antirrhinum* foragers as compared to *Tecoma* foragers. Also as predicted, most of the *Tecoma* foragers fed on both flower types at similar frequencies, whereas most *Lupinus* and *Antirrhinum* foragers specialized on the simple flower type to varying extents. The influence of the degree of complexity on foraging patterns of bees is evident from the runs of consecutive visits, which shortened with experience in complex *Lupinus* flowers, but not in any other flower type.

Individual bumblebee foragers are known to exhibit intrinsic differences in behaviour and foraging patterns (Chittka, Dyer, Bock, & Dornhaus, 2003; Klein, Pasquaretta, Barron, Devaud, & Lihoreau, 2017). We explored the roles of individual foraging experience (initial foraging success, handling times, improvement rates and foraging specialization) and of life history variables (body size, colony stage) as potential predictors of these differences. We found, indeed, that initial success on complex flowers correlated with overall success in *Tecoma* and *Lupinus*. In *Antirrhinum*, on the other hand, colony age but not initial success influenced the total frequency of visits to complex flowers. One of the likely explanations for foragers from growth phase colonies visiting complex *Antirrhinum* more often could be the stable workforce which was large enough to satisfy the colony's demands during this phase. This resulted in some of the bees being more explorative than in other phases. Since we did not see a similar pattern with complex flowers of *Lupinus*, future experiments with regulated colony age will be required to substantiate this possibility. Thus, predicting an individual's tendency to visit complex flowers remains a challenge (see also Muth et al., 2015), but initial success and colony age seem to merit further investigation. Raine and Chittka (2012) demonstrated the adaptive significance of differential learning abilities in foragers. Similarly, the variation observed in the number of bees that specialized on complex and simple flowers in our study is

intriguing when considered at a colony level. Differential propensities and efficiencies of individuals in a range of foraging scenarios might be a good strategy to optimize the overall resource acquisition for a colony (Jandt et al., 2013; Jandt & Gordon, 2016). Mechanisms through which this variation in learning as well as preference for complex tasks translates into the colony's fitness is an interesting area of research requiring additional studies.

Looking beyond social bees, costs and benefits of learning complex handling tactics in pollinators such as hummingbirds, butterflies and flies have received little attention (but see Lewis, 1993; Ramos, Rodríguez-Gironés, & Rodrigues, 2017). Akin to bees, these pollinators can potentially learn to access rewards from complex flowers after several visits (e.g. butterflies handling asclepiad flowers, Ramos, Rodríguez-Gironés, & Rodrigues, 2017). However, this has not been tested in the presence of equally rewarding simple flowers as in our study. Unlike social bees where partitioning of tasks exists, other pollinators need to expend considerable energy on reproductive tasks such as oviposition or finding mates along with foraging. Such constraints may limit the ability of solitary foragers to engage with flowers that require long handling times. Therefore, we predict that in the presence of simple flowers, social bees with individuals restricted to foraging have higher propensities to work their way through morphologically complex flowers. Given the energy expenditure involved, it thus seems that high morphological complexity functions as an exploitation barrier to filter/exclude floral antagonists and inefficient pollinators from the plant's perspective.

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Appendix

Effects of experience

A linear mixed-effects model was run using `lmer()` in R to test the effect of experience on handling time. For this model, we included mean handling time (log transformed) as the response variable, grouped visits (visits as blocks of 10), flower type (complex or simple) and species as fixed effects, and 'Bee ID' nested within species and 'Bee ID' nested within colony identity as random effects. For all the mixed-effects models described, maximal models with interactions were run first, followed by sequential removal of interactive and main effects that were not significant. Using the `anova()` function, we then examined significance for each of the variables in comparison to the null model with the random effect alone. To compare the levels of variables that were significant within each model, we performed post hoc comparisons using the `glht()` function in the `multcomp` package (Hothorn, Bretz, & Westfall, 2008).

Early foraging experience

We tested whether each forager's initial success rate on the two flower types affected its later choices using Spearman correlation tests. Initial success rate was estimated by calculating the proportion of successful visits to complex and simple flower types for each bee's first 15 visits. We used Spearman correlation tests to examine the relationships between initial success rate and proportion of

overall visits, as well as successful visits, to complex and simple flowers. To test whether lower initial handling times on complex flowers were related to frequency of visiting them, we calculated Spearman correlations between the average handling times of each bee's first three successful visits on complex flowers and its proportion of overall visits, as well as successful visits, to complex flowers. Moreover, high rates of improvement in the initial handling of flowers may signal to a bee that such flowers will be profitable after learning and influence its choices. To test this possibility, we considered each bee's first 10 successful visits to complex and to simple flowers. We plotted the log-transformed handling times against visit number separately for complex and for simple flowers and fitted a linear function to each plot. The slopes of the functions provide a measure of the individual's improvement rates on the two flower types, and the difference between the slopes indicates the bee's relative improvement rate on complex versus simple flowers. We used Spearman correlation tests to examine the relationship between the differences in improvement rate (slope) and proportion of successful visits to complex flowers. The effect of early foraging experience was analysed independently of colony age, forager size and foraging specialization. The rationale for this separate analysis was that, since the initial success rate encompasses the first few visits, the appropriate response variable is the individual's later choices. The effects of other sources of individual variation, on the other hand, should be correlated with a bee's choices over its complete sequence of visits.

Table A1
Colony identities and number of bees from each colony

Species	Colony identity	Number of bees (< 35 visits)	Number of bees (> 35 visits)
<i>Tecoma</i>	1	31	9
<i>Tecoma</i>	2	29	15
<i>Antirrhinum</i>	4	15	5
<i>Antirrhinum</i>	5	25	17
<i>Lupinus</i>	3	28	15
<i>Lupinus</i>	4	12	9
<i>Lupinus</i>	2	4	2

Table A2
Bee identities and their visits to damaged complex flowers of *Tecoma*

Bee ID	% Visits to damaged flowers
B32	60
O29	47.6
O36	52
O61	62.71
O68	50.61
O71	44.68
O74	46.82
O81	66.66
W11	52.38
W16	52.43

Table A3
Aims of the tests used in the study and the statistical approaches

Aims	Response variable	Explanatory variables	Statistical test
Innate preference for complex flowers	First visit of a bee		Binomial test
Overall preference for complex flowers	All the visits of a bee		Binomial test
Effect of bee's experience on handling time	Handling time (log- transformed)	Visit number + Flower type (Complex/Simple)+Species+ Bee ID/Species /Colony (random effects)	Linear mixed-effects model
Effects of experience on preference for complex flowers	Percentage overall visits to complex flowers	Experiences/Inexperienced+ Species+ Bee ID/Species /Colony (random effects)	Linear mixed-effects model
Effects of experience on preference for complex flowers	Percentage successful visits to complex flowers	Experiences/Inexperienced+ Species+ Bee ID/Species /Colony (random effects)	Linear mixed-effects model
Handling time of complex vs simple flowers by experienced bees	Differences in handling times of complex and simple flowers after 35 visits		Wilcoxon paired-rank sum test
Specialization (>60% visits) on simple flowers by experienced bees	Percentage visits to simple flowers after 35 visits		One-sample t-test
Extent of variation in individual choices within and between species	Repeatability measure (R, ratio of between-species and within-species variance)		Repeatability test
Variability among foragers	Proportion of overall visits, as well as successful visits, to complex and simple flowers	Individual forager's initial success rate (first 15 visits)	Spearman correlation test
Variability among foragers	Proportion of overall visits, as well as successful visits, to complex flowers	Initial handling times on complex flowers (first 3 visits)	Spearman correlation test
Variability among foragers	Proportion of overall visits, as well as successful visits, to complex flowers	Initial improvement rate on complex flowers (first 3 visits)	Spearman correlation test
Variability among foragers	Percentage overall visits to complex flowers (species-wise)	Colony age (Early/Growth/Late)+Nectar/Pollen forager+ Body size (dry weight in g)	Linear model
Variability among foragers	Percentage successful visits to complex flowers	Colony age	Kruskal–Wallis test
Variability among foragers	Percentage successful visits to complex flowers	Foraging specialization (Nectar/Pollen)	Kruskal–Wallis test
Variability among foragers	Percentage successful visits to complex flowers	Body mass	Spearman correlation test

Table A4
Tukey's post hoc pairwise comparisons

Grouped visits	Estimate	SE	z	P
10-20-<10	-0.47	0.01	-51.57	<0.001
101-110-<10	-1.17	0.02	-55.55	<0.001
111-120-<10	-1.2	0.02	-54.65	<0.001
121-150-<10	-1.2	0.02	-67.51	<0.001
21-30-<10	-0.68	0.01	-68.86	<0.001
31-40-<10	-0.81	0.01	-74.05	<0.001
41-50-<10	-0.96	0.01	-82.03	<0.001
51-60-<10	-1.04	0.01	-81.57	<0.001
61-70-<10	-1.07	0.01	-77.19	<0.001
71-80-<10	-1.15	0.01	-77.45	<0.001
81-90-<10	-1.1	0.02	-67.22	<0.001
91-100-<10	-1.12	0.02	-61.49	<0.001
21-30-10-20	-0.21	0.01	-21.85	<0.001
31-40-10-20	-0.35	0.01	-32.1	<0.001
41-50-10-20	-0.5	0.01	-42.93	<0.001
51-60-10-20	-0.57	0.01	-45.52	<0.001
61-70-10-20	-0.61	0.01	-44.08	<0.001
71-80-10-20	-0.68	0.01	-46.42	<0.001
81-90-10-20	-0.64	0.02	-39.15	<0.001
91-100-10-20	-0.65	0.02	-36.11	<0.001
31-40-21-30	-0.14	0.01	-12.3	<0.001
41-50-21-30	-0.29	0.01	-24.13	<0.001
51-60-21-30	-0.36	0.01	-28.2	<0.001
61-70-21-30	-0.4	0.01	-28.29	<0.001
71-80-21-30	-0.47	0.01	-31.63	<0.001
81-90-21-30	-0.43	0.02	-25.97	<0.001
91-100-21-30	-0.44	0.02	-24.29	<0.001
41-50-31-40	-0.15	0.01	-11.88	<0.001
51-60-31-40	-0.23	0.01	-16.7	<0.001
61-70-31-40	-0.26	0.01	-17.75	<0.001
71-80-31-40	-0.34	0.02	-21.6	<0.001
81-90-31-40	-0.29	0.02	-17.12	<0.001
91-100-31-40	-0.31	0.02	-16.38	<0.001
51-60-41-50	-0.08	0.01	-5.53	<0.001
61-70-41-50	-0.11	0.01	-7.37	<0.001
71-80-41-50	-0.19	0.02	-11.74	<0.001
81-90-41-50	-0.14	0.02	-8.21	<0.001
91-100-41-50	-0.16	0.02	-8.29	<0.001

Table A4 (continued)

Grouped visits	Estimate	SE	z	P
61-70-51-60	-0.03	0.02	-2.14	0.6
71-80-51-60	-0.11	0.02	-6.62	<0.001
81-90-51-60	-0.06	0.02	-3.64	0.01
91-100-51-60	-0.08	0.02	-4.13	<0.001
71-80-61-70	-0.08	0.02	-4.39	<0.001
81-90-61-70	-0.03	0.02	-1.7	0.88
91-100-61-70	-0.05	0.02	-2.34	0.46
81-90-71-80	0.04	0.02	2.29	0.49
91-100-71-80	0.03	0.02	1.36	0.98
91-100-81-90	-0.02	0.02	-0.73	1

Visits were grouped as blocks of 10 for the analysis.

Table A5
Output of mixed-effects models to test the colony effect

Group (Bee ID within colony)	Handling time	Overall visits	Successful visits
Intercept (Base variable: Colony 1)	0.017	5.57	2.08
Colony 2	0.007	12.91	4.81
Colony 3	0.064	2.56	4.61
Colony 4	0.080	6.43	2.52
Colony 5	0.008	0.87	1.65

Standard deviation of random effect (Bee ID nested within colony) used in mixed-effects models, depicting variation in response variables (handling time, percentage overall visits to complex flowers, percentage fed visits to complex flowers) due to colony effect.

Table A6
Correlation matrix of the sources of individual variation

	Improvement rate	Initial success on complex	Initial success on simple	Initial handling time on complex	Colony stage	Bee size	Foraging specialization
Improvement rate	1	0.07	-0.01	-0.43	-0.04	0.16	-0.01
Initial success on complex flowers	0.07	1	0.37	0.29	0.23	0.02	-0.01
Initial success on simple flowers	-0.01	0.37	1	0.27	0.12	0.19	-0.19
Initial handling time on complex flowers	-0.43*	0.29	0.27	1	-0.14	-0.21	-0.04
Colony stage	-0.04	0.23	0.12	-0.14	1	0.04	-0.02
Bee size	0.16	0.02	0.19	-0.21	0.04	1	-0.07
Foraging specialization	-0.01	-0.01	-0.19	-0.04	-0.02	0.07	1

Correlation matrix with strength of correlation (ρ) between the different sources of individual variation pooled across the three species arrays.

* Significant at $P < 0.05$.

Table A7
Correlation tests of early foraging experience with visits to complex flowers

Parameters	Species	ρ	P
Visits to complex flowers: initial success rate on complex	<i>Tecoma</i>	-0.002	0.988
	<i>Antirrhinum</i>	-0.22	0.264
	<i>Lupinus</i>	0.148	0.45
Successful visits to complex flowers: initial success rate on complex flowers	<i>Tecoma</i>	0.409	0.013
	<i>Antirrhinum</i>	0.32	0.11
	<i>Lupinus</i>	0.453	0.017
Visits to simple flowers: initial success rate on simple flowers	<i>Tecoma</i>	0.129	0.45
	<i>Antirrhinum</i>	0.19	0.34
	<i>Lupinus</i>	0.54	0.003
Successful visits to simple flowers: initial success rate on simple flowers	<i>Tecoma</i>	0.62	0.001
	<i>Antirrhinum</i>	0.24	0.21
	<i>Lupinus</i>	0.17	0.392
Visits to complex flowers: initial handling time of complex flowers	<i>Tecoma</i>	0.28	0.18
	<i>Antirrhinum</i>	0.42	0.08
	<i>Lupinus</i>	0.4	0.29
Successful visits to complex flowers: initial handling time of complex flowers	<i>Tecoma</i>	0.2	0.35
	<i>Antirrhinum</i>	0.24	0.34
	<i>Lupinus</i>	0.53	0.14
Visits to complex flowers: improvement rate on complex flowers	<i>Tecoma</i>	-0.22	0.36
	<i>Antirrhinum</i>	0.07	0.88
	<i>Lupinus</i>	0.16	0.67
Successful visits to complex flowers: improvement rate on complex flowers	<i>Tecoma</i>	-0.05	0.79
	<i>Antirrhinum</i>	0.006	1
	<i>Lupinus</i>	-0.16	0.63

Spearman rank correlation tests of early foraging experience (initial success rate, handling time and improvement rate) with percentage overall and successful visits to complex flower types in the three species arrays.

Table A8
Tests showing the relationship between bee size, foraging specialization and colony age with the successful visits to complex flowers

	<i>Tecoma</i>	<i>Antirrhinum</i>	<i>Lupinus</i>
Bee size (ρ)	-0.1	-0.31*	-0.31
Nectar/Pollen (X^2)	0.07	0.06*	0.46
Colony age (X^2)	0.02	5.34	2.26

Nonparametric tests showing the relationship between bee's body mass (bee size), foraging specialization (nectar/pollen) and colony age with the percentage of successful visits to complex flower types in the three species arrays.

* Significant at $P < 0.1$.

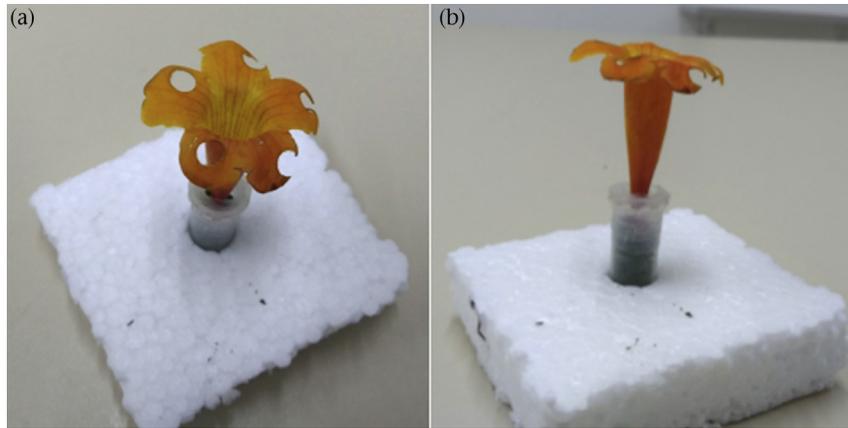


Fig. A1. (a) Top and (b) side view of complex damaged flowers of *Tecoma* x 'Orange Jubilee' with 1 μ l sucrose reward. One bee foraged on four complex intact and four complex damaged flowers in each observation session.

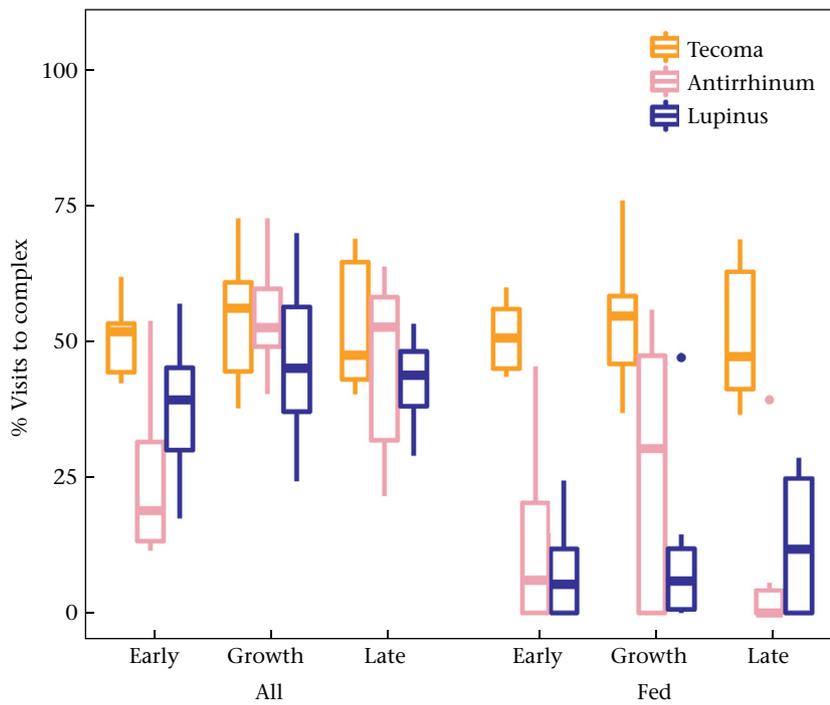


Fig. A2. The percentage of all visits (All) and of successful visits (Fed) to complex flowers by foragers tested during the early, growth and late stages of the colonies in *Tecoma*, *Antirrhinum* and *Lupinus* arrays. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.