



Effects of Experience on Short- and Long-term Foraging Performance in Bumblebees

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Abstract

Honeybees in natural settings show a gradual increase in foraging performance similar to the general pattern of lifetime performance seen in a wide variety of animals including humans. To quantify the factors contributing to such gradual increase in foraging success, we studied bumblebees foraging on pepper plants inside a greenhouse. This allowed us to combine the global measure of the net rate of food delivery to the hive with a detailed examination of bees' performance at flowers over time. Although bees exhibited short-term improvements in foraging ability during their first few foraging trips, we did not observe the predicted long-term increase in performance over days. Our results suggest that a variety of flower-handling tasks, flower choice and movements between plants can be learned quickly under the simple greenhouse settings. The long-term increase in performance under natural settings may be caused by factors including spatial orientation and locating the best plant species, flower patches and individual plants over a large area.

Introduction

The long-term effects of learning on performance are widely appreciated in humans (Ericsson et al. 2006), but have rarely been closely examined in other species. Long-term studies in several bird species have suggested that learning over years contributes to increased reproductive success (e.g. Nol & Smith 1987; Wooller et al. 1990; Daunt et al. 2007; Vieyra et al. 2009). The avian systems, however, are not amenable to the experimental manipulation necessary for critically examining how long-term experience enhances performance.

In a series of studies, Dukas and colleagues (Dukas & Visscher 1994; Schippers et al. 2006; Dukas 2008b) documented in three different field sites and years that honeybees (*Apis mellifera*) foraging in natural settings exhibit a gradual improvement in performance such that they increase their rate of food delivery to the hive over much of their foraging life. Such lifetime performance curves are similar to the

pattern known for birds and mammals including humans (Dukas 1998, 2008a; Helton 2008). Honeybees, however, only showed a rapid improvement followed by a long-term plateau in performance when they were allowed to forage on feeders placed 400 m from the hive, which provided unlimited volumes of sugar water (Dukas 2008a).

The distinct lifetime patterns of performance in natural vs. artificial settings strongly suggested that bees foraging in the field learn a variety of tasks that together contribute to a gradual, long-term improvement in performance. Such tasks could include long-distance navigation, identification of the most profitable plant species, flower patches and perhaps individual plants in such patches, improved movements between flowers and plants, better flower handling techniques and superior motor skills. Evidence for short-term improvements owing to the factors just mentioned exists for both honeybees and bumblebees (e.g. Heinrich 1979; Laverty & Plowright 1988; Capaldi et al. 2000; Cartar 2004; Burns & Thomson

2006; Raine & Chittka 2007, 2008). The effects of long-term experience, however, have been rarely quantified.

To measure the factors that contribute to long-term improvements in performance, we must integrate direct observations on foragers in the field with data on the weight of food delivered and duration of each trip. As we cannot follow individual bees initiating foraging to their chosen flowers in natural settings, we compromised by setting up an experiment inside a greenhouse. Another compromise involved using bumblebees (*Bombus impatiens*), which are more suitable than honeybees for foraging in confined spaces (Shipp et al. 1994; Sabara & Winston 2003; Velthuis & van Doorn 2006).

We attempted to identify what features of bees' foraging behaviour contributed to their overall increase in foraging performance. Specifically, in addition to measuring the weight of floral reward per trip and trip duration, we also video recorded bees from the time they left the hive throughout each foraging trip. We then quantified the durations of orientation flights, flower handling times, lengths of inter-flower flights, frequencies of successive revisits to the same flower and the rate of visits to unrewarding plants. We predicted an overall increase in food delivery rate over a few days and expected both short- and long-term improvements in all the foraging components measured.

Methods

We conducted the research inside a climate-controlled greenhouse (13 × 8 × 5 m in length, width and height respectively) at the Agriculture and Agri-Food Canada Research Centre in Harrow, Ontario in May–June 2009. Temperature and relative humidity were automatically recorded every 15 min. The average (±SE) temperature and relative humidity during data recording (10 AM–4 PM) were 26 ± 0.12 °C and 58 ± 0.6% respectively. The greenhouse chamber was decorated with coloured posters and artificial flowers to simulate a natural setting and to provide distinct landmarks.

We used 64 potted sweet pepper plants (*Capsicum annuum*) grown according to standard commercial practices (Shipp et al. 1994). For ecological realism, the plants were randomly sorted into 15 distinct patches such that there were nine patches of three plants, two patches of five plants, one patch of six plants and three patches of seven plants. The foraging arena was divided into 15 sections and each section was randomly assigned a patch (Fig. 1). This

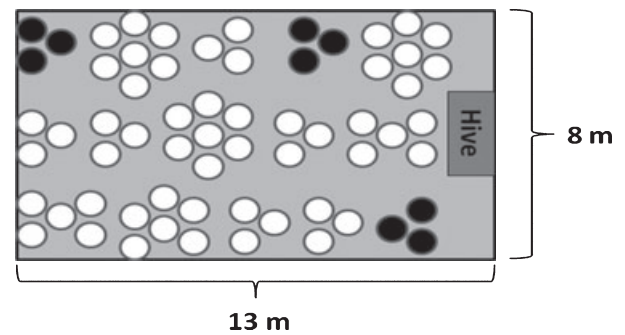


Fig. 1: The distribution of unmanipulated plants (○) and rewardless plants (●) in the greenhouse.

distribution of patches was held constant for the duration of the experiment. The distance between patches was at least 1 m and the distance between adjacent plants within a patch was 0.5 m. Three randomly selected patches of three plants were designated as the 'bad' patches. In these three patches, we removed pollen and nectar from all flowers each morning before the bees commenced foraging. We plucked the anthers from each flower with tweezers and used the rolled up edge of a Kimwipe to remove the nectar while taking care not to damage the flower. Twice per day, a small drop of water was added to each flower so that any newly secreted nectar would be highly diluted.

Preliminary investigations revealed that the average nectar secretion rate per unmanipulated flower was $0.194 \pm 0.035 \mu\text{l}$ per hour (Mean ± SE; 62 recently opened flowers sampled over 3 d, measured from 10 AM to 2 PM, corresponding to peak nectar production). Nectar secretion of the 'bad' flowers was not measured as the added water diluted the sugar concentration of any nectar to effectively zero. Nectar production varied as a function of flower age and time of day (Roldan Serrano & Guerra-Sanz 2004). In the absence of bees, the average nectar volume in 24 flowers on their first day of anthesis was significantly greater than on the following morning ($2.0 \pm 0.27 \mu\text{l}$ vs. $0.3 \pm 0.19 \mu\text{l}$, one-tailed paired-samples *t*-test: $t_{23} = 5.9$, $p < 0.0001$). Indeed, most flowers (20/24) contained no nectar on the second day. The number of flowers varied naturally throughout the experiment with an average of 7.1 ± 0.13 flowers per plant (Mean ± SE; 64 plants measured across 17 d of the experiment). Thus individual 'good' patches exhibited natural variation in quality, but were always more rewarding than the three 'bad' patches. During the experiment, we removed early fruits to promote further blooming.

We obtained a small colony of bumblebees (*Bombus impatiens*) from a commercial provider (Biobest Canada Ltd., Leamington, Ontario, Canada). We monitored the colony's food levels and supplemented it with sugar water (approx. 60% w/w) and pollen when necessary. Before the start of the experiment, we marked all bees with a dot of paint on the thorax at night under red light. On the following day, any of these marked bees seen foraging were removed from the hive. Newly eclosed naïve foragers were uniquely marked upon their first attempt to leave the hive and were subsequently allowed to forage one at a time. A Plexiglas observation tunnel (Dukas & Visscher 1994) was attached to the hive such that the weights of foragers could be recorded and flights restricted as necessary.

On each day, we allowed up to four bees to exit the hive and forage one at a time between 10:00 AM and 4:00 PM. As a result of the limited number of flowers available in the greenhouse, each bee was restricted to three trips per day. We weighed the bees as they departed and arrived at the hive by placing a removable section of the observation tunnel on an analytical balance (AB54-S, Mettler Toledo, Mississauga, Ontario, Canada) with a precision of 0.1 mg. We followed each bee with a handheld digital video camera (DCR-HC42, Sony Handycam, Toronto, Ontario, Canada), dictating plant choice and describing behaviour. A single observer (ZD) moved gently and utilized the camera's zoom function to avoid disturbing the bees.

Following the experiment, we randomized the video files so that the observer was blind to an individual bee's experience and analysed the videos using The OBSERVER 5.0 computer software (Noldus Information Technology, Wageningen, Netherlands). For each trip, we quantified the duration of orientation flights, the duration of each flower visit and the duration of flights between flowers. Orientation flights were defined as the interval between leaving the hive and arriving at the first plant. Flower visits were defined as the entire time a bee was in physical contact with a flower. The sum of orientation flights and the time spent in and between flowers constituted the total trip duration. As a result of the occasional difficulty that our bees experienced in finding the entrance to the Plexiglas tunnel, we considered the end of a trip to occur when each bee left her final foraging patch, thus excluding the time to return to the hive from our analysis. These return flights were always very direct, never lasting more than a few seconds. We also recorded for each trip the frequency of visits to

unrewarding plants, and the frequency of immediate revisits, defined as the number of successive visits to the same flower over the total number of flower visits per trip. We then coupled the detailed video analyses with the data on net weight of food delivery to the hive (arrival minus departure weight) and calculated the net rate of food delivery (net weight divided by trip duration).

We focused on two levels of analysis: (1) Long-term experience over 5 days; and (2) Short-term experience using the first 50 recorded flower visits and first 30 recorded between-flower flights. We recorded an average of 28.7 ± 1.6 (Mean \pm SE) flower visits per foraging trip, meaning that short-term experience often spanned a bee's first few trips. As we allowed only one bee to forage at a time, the short-term experience included all time periods between 10 AM and 4 PM. The data for short-term experience were sorted into blocks of either five flower visits or five inter-flower flights. The data set for long-term experience included five bees that initiated foraging on four different days, and the data set for short-term experience had nine bees that started foraging on seven different days (except for the between-flower flights, which had only eight bees as a result of missing data). The distinct start dates of bees reduced the chance of confounding day effects with experience. Statistical analyses were conducted with PASW Statistics 18 (SPSS Inc., Chicago, Illinois, USA). The analyses involved repeated-measures ANOVAs, using Huynh-Feldt corrected degrees of freedom when assumptions of sphericity were violated.

Results

Long-term Experience

The average daily rate of food delivery did not improve significantly with experience (repeated-measures ANOVA: $F_{4,16} = 0.6$, $p = 0.660$, Fig. 2). Breaking down the rate information into its components, the average net weight of food and mean trip duration also revealed no significant improvement over 5 days ($F_{2,6,10.3} = 0.2$, $p = 0.8$, $F_{4,16} = 1.2$, $p = 0.3$, respectively). The average duration of flower visits ($F_{4,16} = 0.8$, $p = 0.55$), the average duration of flights between flowers ($F_{4,16} = 0.6$, $p = 0.65$) and the frequency of trips to the 'bad' patches ($F_{4,16} = 2.6$, $p = 0.07$) were all unaffected by long-term experience. Further analyses of these measures comparing day 1 with day 5 revealed no significant differences: rate of food delivery ($F_{1,4} = 1.4$,

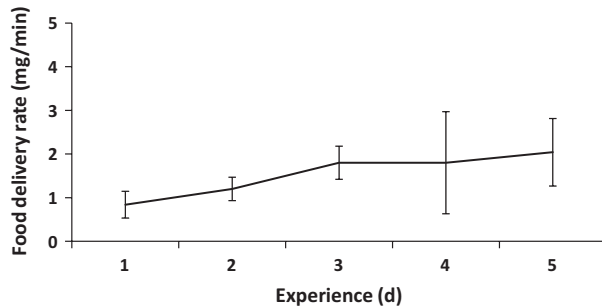


Fig. 2: Mean (\pm SE) rate of food delivery across days ($N = 5$ bees).

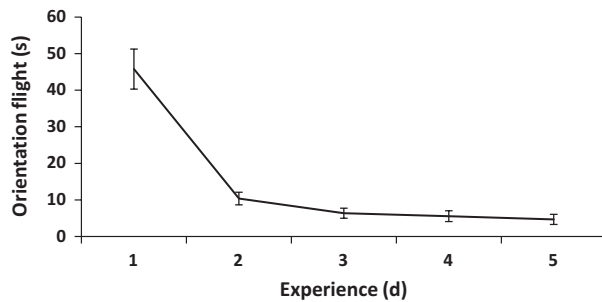


Fig. 3: Mean (\pm SE) orientation flight duration over 5 days of foraging ($N = 5$ bees).

$p = 0.31$), net weight ($F_{1,4} = 0.3$, $p = 0.61$), trip duration ($F_{1,4} = 3.8$, $p = 0.12$), duration of flower visit ($F_{1,4} = 3.4$, $p = 0.14$), duration of flights between flowers ($F_{1,4} = 0.6$, $p = 0.58$) and frequency of trips to bad patches ($F_{1,4} = 5.0$, $p = 0.09$). In contrast, the average duration of orientation flights declined over the 5 days ($F_{4,16} = 68.5$, $p < 0.001$; Fig. 3), and the rate of immediate revisits showed a non-significant decline with experience ($F_{2,1,8,4} = 2.4$, $p = 0.15$; Fig. 4).

Short-term Experience

Experience through the first 50 flower visits resulted in a significant reduction in flower visit duration (repeated-measures ANOVA: $F_{9,72} = 5.8$, $p < 0.001$; Fig. 5). Post hoc within-subject contrasts revealed that much of this improvement occurred within the first 10 flower visits (Bonferroni adjusted for nine comparisons, $\alpha = 0.0056$; visits 1–5 vs. visits 6–10: one-way paired $t_8 = 3.4$, $p = 0.005$). A similar analysis using only the five individual bees included in the long-term data set indicated a comparable short-term improvement in flower visit duration over the first 50 flower visits ($F_{9,36} = 2.8$; $p = 0.012$). Short-term experience was also associated with a reduction

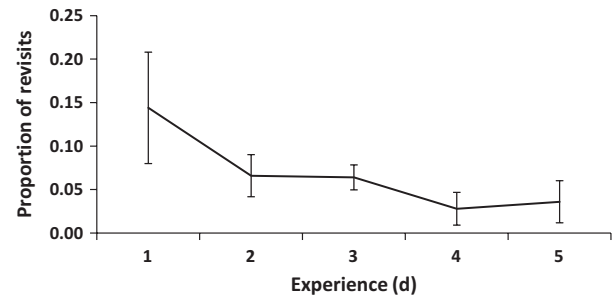


Fig. 4: Mean (\pm SE) rate of immediate revisits ($N = 5$ bees).

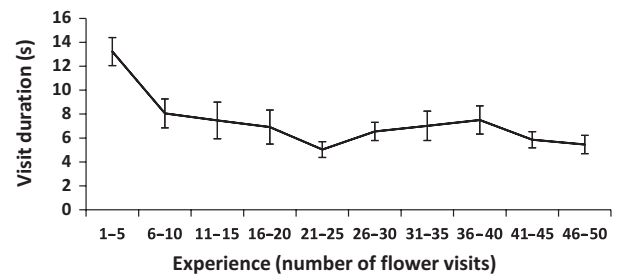


Fig. 5: Mean (\pm SE) flower handling duration. Foraging experience is sorted into blocks of five flower visits ($N = 9$ bees).

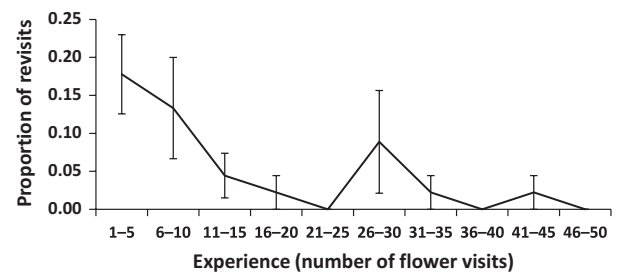


Fig. 6: Mean (\pm SE) proportion of immediate revisits per visit. Foraging experience is sorted into blocks of five flower visits ($N = 9$ bees).

in the rate of immediate revisits (repeated-measures ANOVA: $F_{9,72} = 2.8$, $p = 0.007$; Fig. 6). In contrast, bees showed no significant reduction in the duration of flights between flowers ($F_{5,35} = 1.4$, $p = 0.242$, Fig. 7).

Discussion

Our main goal was to test for long-term improvements in foraging performance and quantify the major contributors to such changes over several days. We found, however, no consistent long-term improvement in the net rate of food delivery to the hive (Fig. 2). Although our analyses indicated

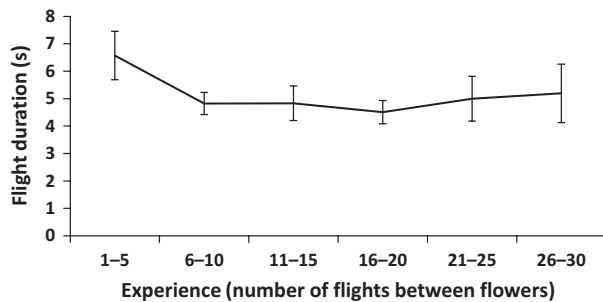


Fig. 7: Mean (\pm SE) duration of flights between consecutive flower visits. Foraging experience is sorted into blocks of five between-flower flights ($N = 8$ bees).

significant reduction in the average duration of orientation flights, this can clearly be attributed to short-term changes over the first few trips (Fig. 3). Such rapid decline in the length of orientation flights is also known in honeybees (Capaldi et al. 2000).

In contrast to the analyses over days, our refined examination of each flower visit indicated that bees rapidly reduced their average flower handling time (Fig. 5). Such short-term improvement has been well documented in bumblebees (e.g. Heinrich 1979; Laverty & Plowright 1988; Laverty 1994; Raine & Chittka 2007, 2008). The bees also quickly improved their ability to orient towards plants as indicated by their reduction in the average frequency of immediate revisits (Fig. 6). Similar overall reduction in revisits was also observed in bees foraging on artificial flowers (Saleh & Chittka 2007). Contrary to our expectation, bees showed no significant short-term reduction in inter-flower flight durations (Fig. 7). It appears, however, that the bees improved over their first several flower visits, but that this improvement was masked by large variation caused by chance differences in inter-flower distances at the vicinity of the flowers visited early on each trip. Although the random spatial distribution of flowers would make locating flowers a prime candidate for long-term improvement owing to learning, the fact that each pepper flower blooms for only 2 d and is mostly rewarding for a single day probably reduces some of the potential for long-term improvements in inter-flower flight durations.

We can think of three explanations as to why the bumblebees did not show the predicted long-term improvement in foraging performance. First, it could be that, unlike honeybees, which took a long time to improve their foraging performance in natural settings (Dukas & Visscher 1994; Schippers et al. 2006; Dukas 2008b), bumblebees can reach their maximal

performance level very rapidly. We believe that this is an unlikely possibility because all species carefully examined under realistic settings show long-term improvements in performance (reviewed in Dukas 1998, 2008a; Helton 2008). Further studies will be necessary to reject this possibility critically.

The other possible explanation for our results is that the bumblebees could reach asymptotic performance after only a few foraging trips because of the relative simplicity of foraging on a single plant species near the hive inside a greenhouse. That is, prior to our experiment, we could readily envision how a few foraging components would contribute to a gradual increase in performance in bumblebees foraging in a small field of pepper plants. Specifically, such factors include identification of the most profitable individual plants (Thomson 1988; Cartar 2004; Burns & Thomson 2006), improved movements between flowers and plants (Ohashi & Thomson 2009) and better flower handling techniques. The current study was restricted to a small number of patches confined to a small area compared with natural bee foraging. This allowed us to conduct detailed observations, but resulted in a relatively low cost of visiting 'bad' patches. This cost further declined as the rewards available in good patches were depleted. A much larger foraging array consisting of multiple plant species with variation in floral complexity arranged into more realistic patches of different species combinations may allow the observation of further long-term improvements. Such a large array, however, would reduce our ability to monitor bees closely.

Finally, it is possible that our failure to detect long-term improvements resulted from a low statistical power. As noted in the results section, however, the same individual bees that showed no significant long-term improvement did show significant short-term improvement. Thus, it is unlikely that we would be able to detect more than a small improvement in performance under our experimental settings even with greater power.

There is good evidence that learning allows bees to reduce flower handling time and reach asymptotic performance after visiting fewer than 100 flowers (e.g. Heinrich 1979; Laverty & Plowright 1988; Laverty 1994). The true measure of foraging performance, however, is the amount of food gathered over time as we have quantified in the current study and previous work with honeybees (Dukas & Visscher 1994; Schippers et al. 2006; Dukas 2008b). Interestingly, perhaps the only other study that examined bumblebees' (*Bombus terrestris*) perfor-

mance measured as floral reward collected over time documented no asymptotic performance even after visiting over 300 flowers (Raine & Chittka 2007). The latter study agrees with our assertion that bumblebees, like honeybees, would show a gradual increase in foraging performance, achieving a peak only after a few days of foraging experience in sufficiently complex settings.

In addition to the factors we could measure in the greenhouse, natural settings add other dimensions of difficulty. First, bees have to locate profitable flower fields, sample a variety of available plant species and then focus on the one or a few most profitable species (Heinrich 1979). Second, unlike the relatively homogeneous greenhouse settings, individual variation in nectar secretion rate within a plant species may be rather high owing to genetic variation and differences in soil type, moisture and herbivory (e.g. Pleasants & Zimmerman 1979; Zimmerman 1981; Nicolson et al. 2007; Kaczorowski et al. 2008). Third, new foragers face a major challenge of locating the best flower patches within perhaps a few kilometres from the nest and navigating successfully back to the hive. Although there have been excellent studies exploring bees' spatial orientation (e.g. Osborne et al. 1999; Capaldi et al. 2000; Menzel et al. 2005), we still do not know whether long-term navigational experience allows bees to locate farther and more profitable food sources. Our results still leave open the possibility that spatial learning and navigational improvements on such a large scale may be the driving force behind the performance curves observed in natural settings (Dukas 2008b).

In sum, our attempt to link long-term improvements in foraging performance observed in natural settings with controlled observations in the greenhouse have failed because bees under the simpler settings showed rapid improvement in foraging ability. Our results suggest that long-term improvements in foraging success may be related to complex tasks including spatial orientation and learning to favour the best plant species, patches and individual plants over a large area.

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