

Overnight memory retention of foraging skills by bumblebees is imperfect

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Abstract. Newly emerged bees learn to forage more efficiently as they gain experience. To test the hypothesis that foraging efficiency would increase as bees gain experience during the day, but would decrease after a night, owing to loss of memory, naive *Bombus terrestris* bumblebees were allowed to forage on two clusters of artificial flowers of unequal profitabilities during 3 consecutive days. Nectar intake rate, percentage of visits to the more profitable cluster, probing time and time intervals between visits were computed as measures of the bees' foraging efficiency. Nectar intake rates increased significantly during the day, and decreased partially but significantly after a night. They varied greatly between bees. The bees did not show a preference for one of the clusters at the onset of the experiment, and none consistently increased their visits to the more profitable cluster during single observation days. Most individuals did not visit the higher-reward cluster exclusively by the end of the third day. However, visits to the higher-reward cluster did increase significantly when the first day of observation was compared with the third day. Preference for the higher-reward cluster increased after the first night but decreased significantly after the second night. Probing time and inter-visit intervals decreased significantly during observation days, and increased significantly after a night. The results indicate that bees learn to approach and probe flowers faster, as they gain experience, during a foraging day, but that these skills are partially forgotten overnight. Patch preference is formed more slowly. Once formed, it is also weakened overnight. Such partial forgetting may aid the bee in reacting quickly to overnight changes in resource profitability by modifying flower choices and handling techniques.

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Experienced generalist bees exploit high-rewarding flower types more frequently than inexperienced bees (Heinrich 1979; Waddington & Holden 1979; Menzel 1985; Dukas & Real 1993; Gould 1993; Menzel et al. 1993), and work flowers faster (Heinrich 1979; Laverty 1980, 1994; Laverty & Plowright 1988). While this increase in foraging proficiency during a single observation session is well documented, it is less clear how foraging efficiency changes over a period of several days, and over night periods. Dukas & Visscher (1994) showed that the net rate of forage uptake by honey bees, *Apis mellifera*, increases gradually over the first 7 days of foraging, but were not able to identify the causes for this increase. Evidence from a few other studies indicates that bees

remember floral preferences overnight: Menzel (1968) showed that honey bees trained to fly to a coloured target continued to choose the same target for several days afterwards. Heinrich et al. (1977) and Dukas & Real (1991) found, in laboratory studies, that bees retained overnight the colour preferences they had formed on the preceding day. Dukas (1987) studied visits of unmarked bees to rewarding male flowers of *Echballium elaterium* and to unrewarding female flowers which mimic them. He found that honey bees discriminated better between the model and the mimic, at the beginning of the foraging day, than did two species of solitary bees. He attributed the difference to the superior overnight memory capabilities of honey bees. However, these studies did not characterize the changes in the bees' choice performance, and especially the changes in flower handling competence, over several days. Moreover, the bees' previous foraging history was not known.

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In the present study we followed the development of foraging skills in marked, inexperienced bumblebees, *Bombus terrestris*, which foraged on artificial flowers in the laboratory over a period of 3 days. Each individual had to rely on its own experience when making foraging decisions, since bumblebees do not communicate with nestmates about food sources. We eliminated the effects of reward variability, temporal reward fluctuations and intraspecific competition on the bees' preference formation. We recorded the bees' flower choices, as well as the time they allocated to nectar imbibing and flight. We were thus able to relate acquisition rate of foraging skills to previous experience by comparing changes in foraging efficiency over the first, second and third days. We also characterized overnight changes in the bees' preferences and foraging efficiency. These data were used to test the following hypotheses: (1) foraging efficiency, measured as gross nectar intake per unit time, increases over each foraging day; (2) this increase is due to more frequent visits to high-rewarding flowers, faster handling of the flowers and faster flight between them; and (3) foraging efficiency diminishes after a night because of diminished preference for high-rewarding flowers, and decreases in the bees' flower handling abilities.

METHODS

Experiments were carried out in a 3×4 m flight room. Temperature ranged from 26 to 30°C and relative humidity was 40–70%. The room was illuminated during 0630–1830 hours. We conducted observations during August and September 1994, between 0630 and 1530 hours.

We obtained a colony of naive bumblebees from Kibbutz Yad-Mordechai, Israel. Workers were marked with numbered plastic tags on the day when they first flew out of the colony. Pollen was supplied ad libitum, directly to the colony. All of the bees were allowed to feed on a 50% sucrose solution, which was provided in a transparent feeder, for 3 h after observation sessions. They were then starved until the next session, on the following morning.

During experiments, a single, untrained bee was allowed to forage on 20 artificial flowers with an orange landing surface, and 20 flowers with a violet landing surface. The flowers were arranged

in two spatially distinct clusters or 'inflorescences' on a table of 1.4×2.4 m. We created differences in colour, location and shape of landing surface between the two flower types so as to facilitate their identification for the bees. The orange flowers were randomly placed in 20 out of 30 possible positions in one corner of the table. Similarly, we assigned the violet flowers to 20 of the 30 possible positions in the diagonally opposite corner. The distance between pairs of flowers within a cluster was 43.72 ± 7.87 cm ($\bar{X} \pm \text{SD}$), and between clusters 120.08 ± 24.76 cm. Thus, after leaving a flower, the bee could either fly to another flower of the same type or shift to the other patch. The orange flowers ('poor' patch) offered the bee $0.33 \mu\text{l}$ of a 30% sugar solution at each visit, while the violet flowers ('good' patch) offered $1 \mu\text{l}$ of the same sugar solution. Real flowers have similar nectar volumes (e.g. Kadmon et al. 1991; Shreiber 1993). The orange landing surface was lobed, while the violet landing surface was round. The artificial flowers were covered, invisible and inaccessible to the bees between observation sessions. Each artificial flower included a photo detector, which allowed automatic recording of flower number, the time when the bee inserted its head and the time it withdrew its head for each foraging visit. Flowers were automatically refilled ca 2 s after the bee had flown away. Thus, bees that returned to previously visited flowers were always rewarded. Refilling did not induce the bees to remain on the flowers, and did not interfere with their activity. As, in preliminary experiments, no measurable nectar was left after the bees had visited the flowers we did not measure residual nectar.

The first bee that flew to the artificial flower patch and started foraging was allowed to visit the flowers, while other individuals that tried to forage simultaneously were caught and set aside. The bee was removed at the end of 150 flower visits. The landing surfaces were then wiped carefully with a water-moistened paper towel to remove odour markings (Schmitt & Bertsch 1990; Giurfa 1993). The captive bees were released, and another bee was allowed to approach the flowers. If a bee returned to forage on the next day, it was allowed to make another 150 visits, and the same procedure was repeated on the third day. We observed 14 marked bees which visited the flowers on 3 consecutive days. The 150 visits were generally made within 1 h or less, in the course of two or three foraging bouts.

Data Analysis

We calculated changes in colour choice performance, probing time and inter-visit intervals over time. Probing time was defined as the time between a bee inserting and withdrawing its head from a flower. Inter-visit intervals were defined as the time between a bee withdrawing its head from one flower and inserting it in the next flower. This time is made up of flight to the next flower, and handling of the flower before the bee inserts its head. Nectar volume imbibed during a visit, divided by the time until the bee inserts its head into the next flower, was defined as nectar intake rate for that visit. As nectar intake rates, probing times and inter-visit intervals, measured for a series of flower visits of one bee, are not independent variables, we calculated standard errors using cluster sampling methods (Steel & Torrie 1981), where all measured values of a variable for a single bee were treated as one cluster.

We used procedures CORR, REG and TTEST of SAS 6.04 software (SAS Institute 1988) for some of the statistical analyses.

RESULTS

Nectar Intake Rates

Figure 1 shows nectar intake rates, averaged over groups of 10 consecutive visits for all bees. The change in nectar intake rate during each day of the experiment was estimated through linear regression, for each bee separately. Regression slopes ranged from 1.57×10^{-4} to 18.04×10^{-4} $\mu\text{l/s}$ per 10 visits for day 1, 1.56×10^{-4} to 12.86×10^{-4} $\mu\text{l/s}$ per 10 visits for day 2, and -1.13×10^{-4} to 9.83×10^{-4} $\mu\text{l/s}$ per 10 visits for day 3 of the experiment. Regression slopes were positive for all bees in the first 2 days of observation, and for 12 of the 14 bees during the third day. This indicates that foraging efficiency generally increased during foraging days. A null hypothesis, that increases and decreases in foraging efficiency are equally likely, can therefore be rejected (sign test, $P < 0.001$ for days 1 and 2, $P = 0.012$ for day 3). Inspection of the regression parameters suggested large differences in learning rate of foraging skills among bees. Regression slopes indeed varied significantly between individuals (test for homogeneity of slopes, $P < 0.001$ for all 3 days, Steel & Torrie 1981), so that they could not be pooled for further analysis.

We calculated the mean nectar intake rates for the beginning (flower visits 1–10) and the end (visits 140–150) of each observation day, for each bee separately (Table I). We then tested for changes in nectar intake rate within and between days through paired *t*-tests. Nectar intake rates increased significantly during each of the three observation days ($P < 0.001$ for days 1–2, $P < 0.01$ for day 3) and decreased significantly after the two intervening nights ($P < 0.05$ for the first night, $P < 0.001$ for the second night). The decreases in nectar intake rates following a night were only partial, since nectar intake rates at the beginning of day 2 were significantly higher than at the beginning of day 1 ($P < 0.001$). Similarly, nectar intake rates at the beginning of day 3 were significantly higher than at the beginning of the previous day ($P < 0.001$). Nectar intake rates at the end of day 2 and at the end of day 1 were not significantly different ($P = 0.1$). Neither were nectar intake rates at the end of day 2 and at the end of day 3 ($P = 0.096$). This suggests that the steady-state nectar intake rates were already attained by the end of day 1. The improvement in nectar intake rates during the second day of the experiment was smaller than during the first day ($P < 0.001$), and the increase during day 3 was even smaller than during day 2 ($P < 0.001$).

Next we tested whether the overall increases, and overnight decreases, in nectar intake rates were due to changes in the bees' colour choice frequencies, flower handling proficiency, or both.

Colour Choice Performance

We counted the number of visits to violet (more rewarding) flowers, made by each bee within its first 50 visits, and calculated an average value for the 14 bees (this is equivalent to cluster sampling with clusters of identical sizes). The percentage of visits to violet was $50.86 \pm 7.88\%$ ($\bar{X} \pm \text{SE}$), indicating no innate preference for one of the presented colours. We calculated the number of visits to violet flowers for each bee on days 1, 2 and 3 of observation (Table II). On the first observation day, only 53% of the visits were in the good patch. The percentage of visits to the good patch increased significantly between the first and second day of observation (one-tailed, paired *t*-test: $P < 0.05$), but did not change significantly between day 2 and day 3 (one-tailed, paired *t*-test). We tested for each bee, separately for each day, whether visits to violet flowers were correlated

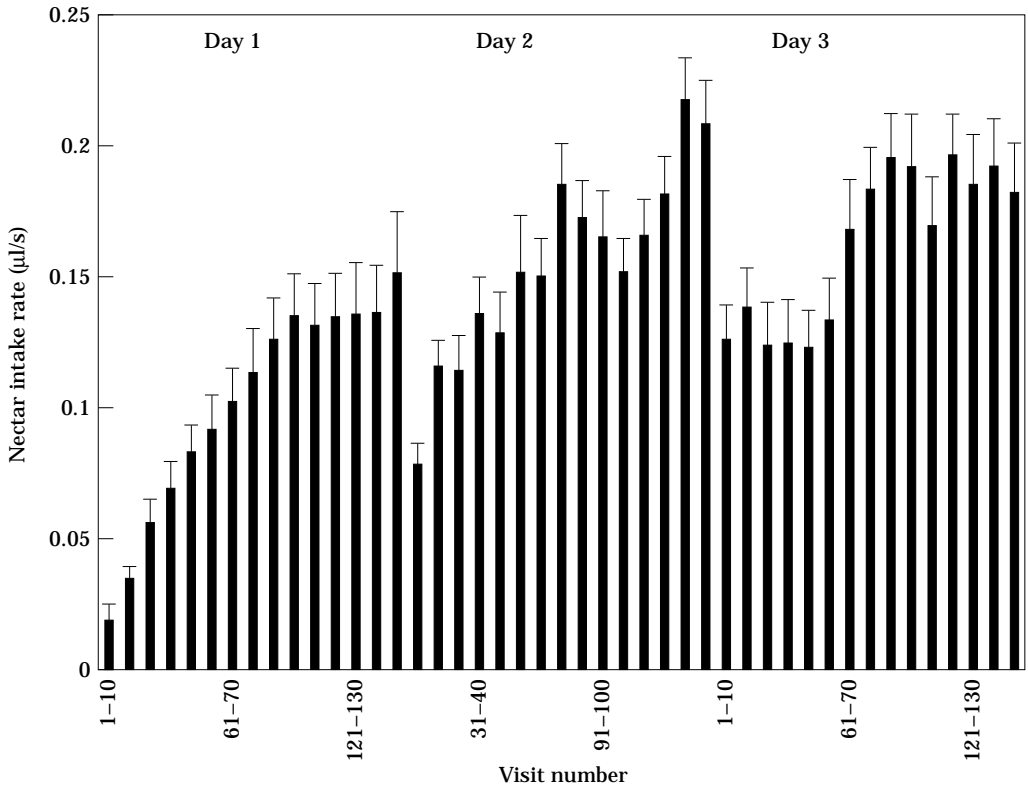


Figure 1. Mean nectar intake rates for groups of 10 visits during the 3 days of the experiment. Error bars are 1 SE.

Table I. Mean \pm SE nectar intake rates (in $\mu\text{l}/100$ s) for the first 10 visits and the last 10 visits of each observation day

	Visits 1-10	Visits 140-150
Day 1	1.69 ± 0.60	14.97 ± 2.35
Day 2	7.61 ± 0.79	20.45 ± 1.70
Day 3	12.11 ± 1.44	18.16 ± 1.88

with visit number (Spearman rank correlations). In this manner we examined whether preference for the good patch increased in the course of single observation days. Correlation coefficients varied so widely between bees and observation days that they could not be pooled (Snedecor & Cochran 1967). In some of the cases the correlation was positive (i.e. visits to the good patch increased during the course of a day), while in

Table II. Percentage of visits ($\bar{X} \pm \text{SE}$) to the high-rewarding patch

	All 150 visits	First 50 visits	Last 50 visits
Day 1	53.19 ± 7.37	50.86 ± 7.88	53.00 ± 10.16
Day 2	72.86 ± 3.12	64.71 ± 7.68	75.29 ± 5.04
Day 3	70.21 ± 5.80	64.00 ± 5.78	74.29 ± 6.18

Values are means for 14 bees.

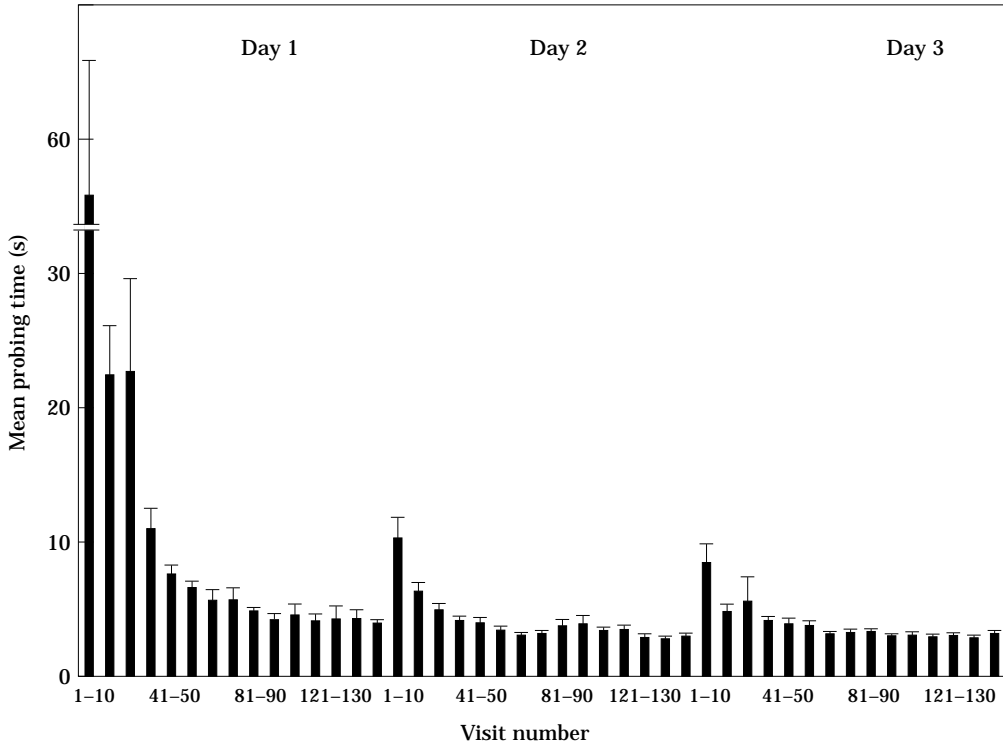


Figure 2. Mean probing times for groups of 10 visits, during the 3 days of the experiment. Error bars are 1 SE.

others it was negative. We conclude that preference for the ‘good’ patch was sometimes, but not always, formed in the course of the 150 daily flower visits.

To test whether colour choice performance weakened overnight we examined whether the good patch was visited more often at the end of a foraging day than at the beginning of the next day. Switches between patches were less frequent than expected at random (runs test: $P < 0.001$), and the mean \pm SE run length was 8.929 ± 0.621 consecutive visits to a patch. We therefore could not rely, in this case, on colour choice in the first and last 10 flower visits as an indication of patch preference. Instead, we divided each daily observation into an initial foraging phase (visits 1–50), a middle phase (visits 51–100) and a final phase (visits 101–150). We compared the percentage of visits to the good patch in the final phase of one day with the initial phase of the following day. Choice of the good patch increased non-significantly over the first night but decreased

significantly (one-sided, paired t -test: $P < 0.05$) over the second night (Table II).

Probing Times and Inter-visit Intervals

Probing times and inter-visit intervals were longest on day 1 and shortest on day 3. They also decreased at a non-linear, decelerating rate over the course of each day of observation (Figs 2, 3), most steeply on day 1, more moderately on days 2 and 3. We did not find a simple transformation to make these data linear, and thus could not compare regression parameters between observation days. Instead, we compared, through paired t -tests, mean probing times and inter-visit intervals at the beginning (first 10 visits) and the end (last 10 visits) of each observation day (Tables III, IV).

Probing times and inter-visit intervals decreased significantly ($P < 0.001$) over the course of each observation day. The decrease in probing time on day 1 was larger ($P < 0.001$) than on day 2, but the decreases during days 2 and 3 did not differ

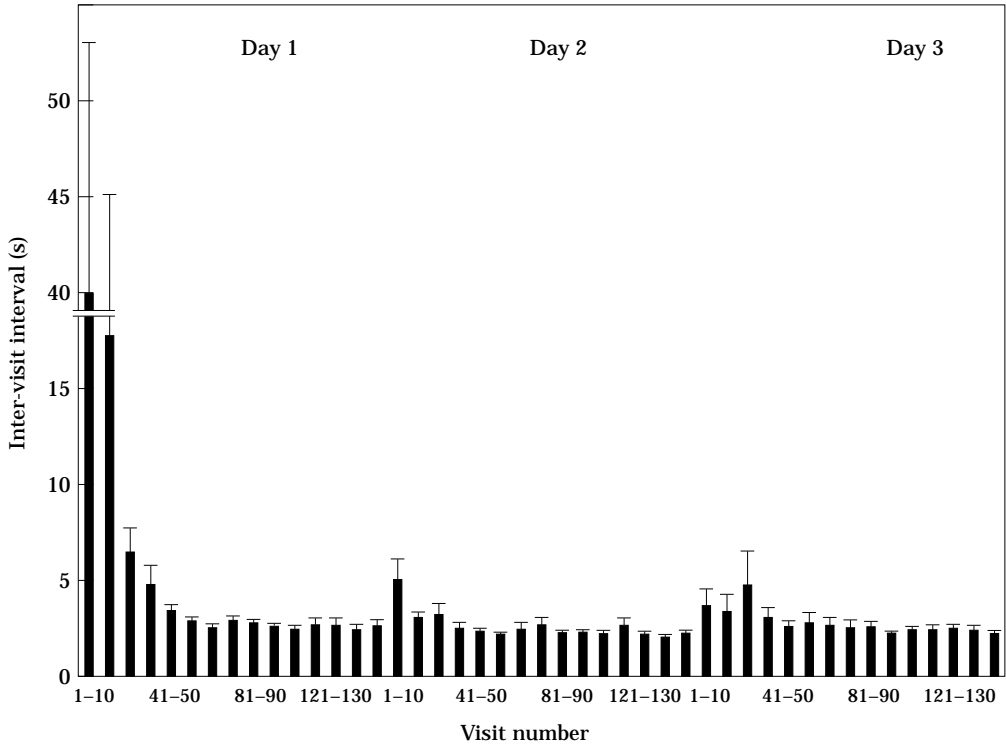


Figure 3. Mean inter-visit intervals for groups of 10 visits, during the 3 days of the experiment. Error bars are 1 SE.

Table III. Mean \pm SE probing time (s) for the first 10 visits and the last 10 visits of each observation day

	Visits 1-10	Visits 140-150
Day 1	56.12 \pm 18.97	4.09 \pm 1.18
Day 2	10.27 \pm 3.21	3.16 \pm 0.51
Day 3	8.32 \pm 2.22	3.20 \pm 0.59

Table IV. Mean \pm SE inter-visit intervals (s) for the first 10 visits and the last 10 visits of each observation day

	Visits 1-10	Visits 140-150
Day 1	41.18 \pm 21.09	2.39 \pm 0.63
Day 2	5.68 \pm 2.72	2.16 \pm 0.36
Day 3	5.13 \pm 3.59	2.21 \pm 0.41

significantly. Similarly, the decreases in inter-visit intervals were larger on the first day than on the second day of the experiment ($P < 0.05$), but similar on days 2 and 3.

Probing times and inter-visit intervals were significantly shorter at the beginning of day 2 than at the beginning of day 1 ($P < 0.001$), but did not differ significantly between the first 10 visits of days 2 and 3. Probing times increased significantly between the end of day 1 and the beginning of day 2, and between the end of day 2 and the beginning of day 3 ($P < 0.001$). Inter-visit intervals also increased significantly after both nights ($P < 0.01$).

The mean probing time at the end of day 1 was significantly longer than at the end of day 2, but probing times did not differ significantly between the end of day 2 and the end of day 3. Differences in inter-visit intervals between the end of days 1, 2 and 3 were not significant.

Individual Behavioural Variation

The individuals in our study clearly varied in their learning and memory capabilities, regarding colour choice performance, and the efficiency of probing and flight (see Fig. 4 for an example of

individual differences in nectar intake rates). A possible interpretation of this variability is that some bees (the 'fast learners') acquired all the foraging skills faster than the others (the 'slow learners'). According to this hypothesis, individuals that choose the good patch most often are also expected to imbibe nectar most efficiently, and fly between flowers most competently. The percentage of visits to the good patch was indeed significantly correlated (Pearson correlation: $r = -0.541$, $N=14$, $P<0.05$) with the mean final probing time (visits 141–150) on the first day of the experiment. However, the correlation was not significant on days 2 ($r=0.004$) and 3 ($r = -0.250$). The correlation coefficients between percentage of visits to the good patch and inter-visit intervals were -0.234 , -0.203 and 0.277 for days 1, 2 and 3, respectively. None of these coefficients was statistically significant. Thus it seems that 'fast learners' of colour differences are not necessarily 'fast learners' of other foraging skills.

Next we examined whether age differences between the experimental bees may account for some of the observed behavioural variation. We used the date on which the bees were marked as a rough estimate of their emergence date, and correlated the bees' age with percentage choice of the good patch. The correlation coefficients (Pearson correlation, $N=14$) were 0.144 for day 1 of the experiment, 0.006 for day 2 and 0.080 for day 3, $P>0.05$ for all three days. This suggests a weak effect of age on colour choice performance.

DISCUSSION

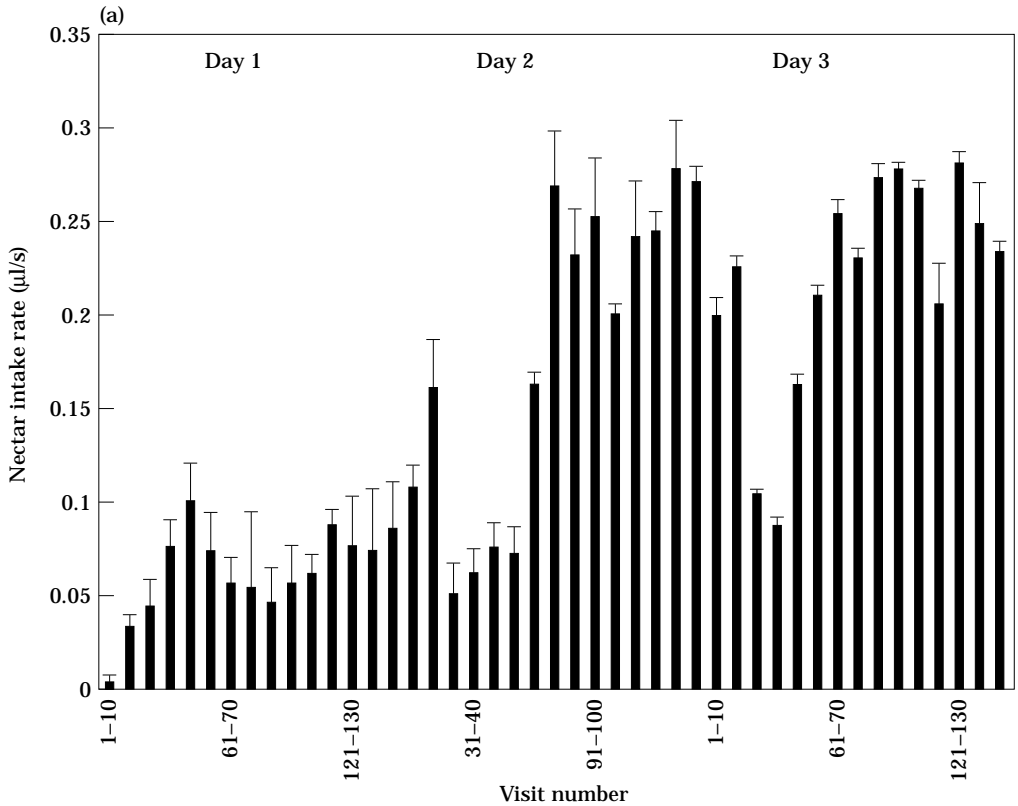
Our results indicate that the bumblebees became more efficient foragers as they gained foraging experience: most of them chose the good patch more often, and all of them required less time for nectar probing and for travelling between flowers. Probing time probably becomes shorter because the bees learn the flower morphology, and what size of nectar drop to expect within the flower, as they gain experience. Transition time between visits may shorten as a search image for the flowers is formed (Greggers & Menzel 1993), and as the bees learn to take the shortest flight routes. The bees also learn where to insert their heads to obtain a reward, so that they spend less time on

the flowers before inserting their heads (Laverty 1994). This may lead to a further decrease in inter-visit interval. As the bees warm up during flight, general metabolic and activity rates may increase, contributing to the acceleration in flight and flower handling over a foraging day. However, Heinrich (1993) showed that body temperatures of bumblebees are considerably elevated before the beginning of flight through shivering thermogenesis. Therefore we expect that further warming up during flight did not have a major effect on activity rate.

As expected, bees became more efficient nectar collectors during the course of the day, but lost some of this proficiency overnight. Nectar intake rates continued to increase even over the third day of observations. This improvement resulted from faster flight, flower handling and imbibing. However, colour preference did not increase significantly and consistently over any one day, and decreased during the second, but not over the first night. In several laboratory studies on bumblebees, colour preference of over 80% was attained during ca 150 visits (Dukas & Real 1993), but the quality difference between the 'good' and the 'poor' flowers in those studies was larger than in the present study. Possibly the 150 daily visits that we allowed the bees were not sufficient, under our conditions, to form a strong colour preference during a daily observation session.

Visits to the good patch reached 74% at the end of the third day. Nine of the 14 observed bees foraged on the artificial flowers and were observed for a fourth day. These bees made only $59.3 \pm 20.61\%$ ($\bar{X} \pm \text{SD}$) of their visits to the more profitable patch on the fourth day. Thus, even experienced bees continued to sample the poorer patch fairly often. Incomplete specialization on the most rewarding flower species ('majoring' and 'minoring') has also been described for bumblebees foraging under natural conditions (Heinrich 1979).

We observed much variability between individuals in colour choice performance, probing durations and travel durations. Examination of individual records suggests that age differences, and differences in probing skills or flight skills, did not strongly affect the variability in our bees' colour-choice abilities. This variability is probably a product of several inherited and environmental factors, which are still to be elucidated. Cohen (1993) pointed out, in a theoretical study, that the

**Figure 4a.**

optimal level of dietary specialization in foragers is expected to depend on the variance in quality among available food sources. This variability is, in turn, affected by the foragers' feeding choices, and may therefore change with time. According to this reasoning the observed variability in patch specialization among our bumblebee workers may be of adaptive value to the whole colony. Within-colony variability in dietary specialization levels may be necessary for the efficient exploitation of food sources, if the variance of quality among food sources fluctuates over time.

Handling rates, as expressed by probing time and inter-visit intervals, decreased over a day similarly to Laverty's (1980, Laverty & Plowright 1988) observations on handling of real flowers by bumblebees. Inter-visit intervals were similar at the end of each observation day, and probing times did not differ significantly between the end of day 2 and the end of day 3. This suggests that the bees approached their steady-state handling

speed by the end of day 2. Nevertheless, they lost some of these handling skills overnight. This finding contrasts with Woodward & Laverty (1992), who found no decrease in handling efficiency in bumblebees that attained maximal handling velocity, and were then prevented from foraging for a day.

Our results agree with previous demonstrations that long-term memory exists in bees (Wahl 1932; Menzel 1968; Koltermann 1971; Gould 1987), but indicate that this memory can be imperfect. Since the relative abundance and profitability of flowers in a natural situation may change daily (Waser 1983; Zimmerman & Pyke 1986; Real & Rathcke 1988), it may be selectively advantageous for a bee partially to ignore information collected on previous days. This would lead the bee to try several food sources every day, rather than specializing completely. Such a strategy may be particularly adaptive for newly emerged bees, which have very little information on the relative profitability of

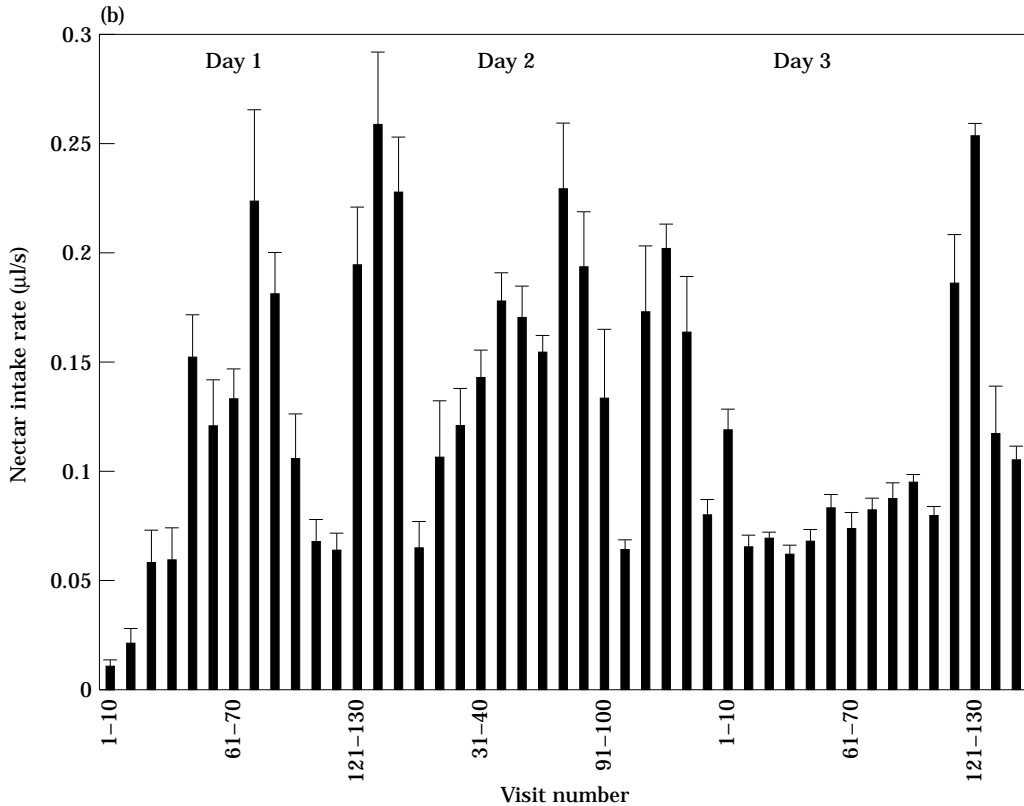


Figure 4b.

Figure 4. Mean nectar intake rates of two bees. Nectar intake rates in (a) are for the bee that formed the strongest specialization on the high-reward cluster, and in (b) are for the least specializing bee in the experiment. Means for groups of 10 visits, for the 3 days of the experiment, are plotted. Error bars are 1 SE.

available food sources. Partial inattention to past experience could also help experienced bees to respond to changes in their environment (Real et al. 1990; Real 1991).

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