

## Lifetime learning by foraging honey bees

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*(Received 2 August 1993; initial acceptance 7 August 1993;  
final acceptance 28 September 1993; MS. number: A6651R)*

**Abstract.** It is usually assumed that insects invest little in learning because of their short life span. However, the relative time and energy invested in learning should reflect the potential costs and benefits of learning regardless of absolute life span. As a first step in evaluating lifetime aspects of learning in insects, learning by individual honey bee, *Apis mellifera*, foragers was assessed based on their foraging success from inception of foraging until death. The net rate of forage uptake by new foragers was low and gradually increased to approximately twice the initial rate after a week of foraging. This period coincided with the median life span of the foragers. Hence, forager honey bees apparently spend a considerable portion of their life span learning and improving their foraging skills.

Students of learning commonly assert that insects have limited cognitive abilities due to their short life span and small body and brain sizes (Mayr 1974; Johnston 1982; Staddon 1983). The life of insects and other animals may be perceived as involving a trade-off between spending time and energy learning new things, and exploiting things already known (Staddon 1983). Therefore, the notion that short-lived insects should spend little time learning is intuitively appealing. An alternative and less biased approach, however, is to consider the potential benefits and costs of learning in predicting the relative time spent on learning regardless of an animal's absolute life span (Dukas & Real 1993).

Small body and brain sizes also may limit cognitive capacity. However, the increasing understanding of relatively sophisticated learning abilities in insects, especially social bees, challenges this notion (Menzel et al. 1974, 1993; Gould & Gould 1982, 1988; Bitterman 1988; Couvillon & Bitterman 1991; Real 1991; Papaj & Lewis 1993). Nevertheless, most learning experiments on insects are usually very short in temporal scale even relative to the insects' life spans.

As a first step in evaluating lifetime learning capacity in insects, we monitored the foraging success of individual honey bees, *Apis mellifera*, from the time they initiated foraging until they

died. Because forager honey bees are exclusively engaged in their foraging task, we could readily relate success in collecting food to overall foraging experience. As a measure of foraging success, we used the currency of the net rate of uptake of floral reward (Pyke 1984; Stephens & Krebs 1986). This measure is only an indirect estimate of learning but it has the powerful advantage of allowing bees to learn under their natural settings rather than under more controlled but artificial laboratory settings.

We wished to distinguish between two alternative lifetime learning schemes. In the first scheme, naive bees learn relatively little over their lifetime; they learn a foraging task on their first few foraging trips and then reach a plateau in foraging performance, which eventually declines due to senescence. In the second, bees continue to increase their foraging performance for most of their overall life span, before reaching senescence.

## METHODS

We conducted the experiment at the agricultural station of the University of California, Riverside, in November 1992. All days during the experiment were sunny, with daily high temperatures ranging between 15 and 25°C. Forage was relatively scarce in this season; a nearby large honey bee colony mounted on a balance lost weight during the experiment at a fairly slow and steady rate of 230 g/day.

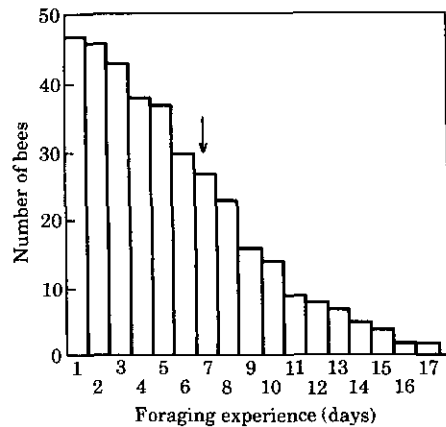
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We allowed bees to emerge in an incubator, marked them with individually numbered plastic tags (Opalithplättchen) and introduced them into a two-frame observation hive containing about 3000 bees. We made three introductions of 40 bees each 3 days apart. The observation hive was set up in the laboratory and a 50 cm transparent Plexiglas tunnel provided the bees access to the outdoors. A 5-cm-long portion at the centre of the tunnel could be gated at each side and removed. In this removable cage, we individually trapped each marked bee and weighed her on an analytical balance each time she either left the hive on a foraging trip or arrived back. The analytical balance, with precision of  $\pm 0.1$  mg, reported the bee's weight directly to a computer; to increase accuracy, the computer averaged at least five sequential weight readings. The computer recorded the time of day, and we added information about (1) the bee's identification number, (2) her direction, either exiting on a foraging trip or returning to the hive and (3) the amount of pollen the bee carried (0: no pollen; 1: small loads; 2: full pollen loads).

We used the computer record to calculate trip time, net weight of forage uptake, and net rate of forage uptake for each foraging trip by each bee. Our method of measuring net rate of forage uptake has two minor weaknesses. First, we could not determine forage quality, that is, nectar concentration. Second, we could not account for short-term changes in a bee's weight unrelated to the amount of forage she carried. For example, bees could lose more water during longer foraging trips. Nevertheless, our method is useful for examining long-term foraging patterns by individual bees.

Two weeks after introducing the bees into the hive, we began observations. On the first day, we removed a few marked bees that were already foraging. On the next day, we began to record and weigh all marked bees departing and returning to the hive. These observations continued all day long, from the time bees began foraging early in the morning until they ceased late in the afternoon. We continued our observations for 20 days excluding 2 days with strong winds and no foraging activity; this left us with a total of 18 observation days.

We recorded data for 47 bees, including 33 individuals with complete lifetime records, and 14 individuals that were still alive by the end of the



**Figure 1.** The number of individual honey bees observed and their foraging experience. Included are 33 individuals with complete lifetime records, and 14 individuals that were still alive by the end of the experiment. The arrow denotes the median length of foraging span among bees that died during the experiment.

experiment (Fig. 1). Bees that died before the termination of our experiment had a mean ( $\pm$  SE) foraging span of  $7.7 \pm 0.75$  days, median of 7 days, and range of 2–17 days ( $N=33$  bees; unpublished data). Before initiating foraging, naive bees usually leave the hive on short orientation flights (Ribbands 1952; Vollbehr 1975). We excluded these and other trips of less than 5 min from our analysis. Therefore, what we included as the first foraging trip of each new forager was a trip that usually lasted more than 15 min. In less than 1% of cases we failed to record the time and/or weight of a bee exiting or returning. In those cases where an individual had consistent foraging times and/or weights for several trips on each side of the missing datum, we inferred the missing value. Where such reconstruction was not obvious, we treated this lost information as a missing value.

We were interested in the association between long-term experience and foraging success. Foraging experience may be measured as number of foraging trips, foraging time in hours, or the number of foraging days. Here we present our results in terms of the number of days as the temporal scale. This is because 'day' is a natural and biologically meaningful unit of time. Our analyses at the other two temporal scales had nearly identical results to the analysis based on number of days.

The net rate of forage uptake could be influenced by factors other than experience. To

separate variation in forage uptake due to other factors from that owing to experience, our ANOVA model included factors of day, time of day, and the type of forage (nectar or pollen), as well as experience (number of days foraging). Bees initiated foraging on different days during the experiment; 25 bees began foraging during the first 9 days, and 22 bees initiated foraging during the last 9 days of the experiment. Therefore, the effects of daily forage availability could be easily separated from those of foraging experience. Furthermore, although the effect of day was significant ( $P < 0.05$ ), there was no pattern of consistent increase or decrease of mean daily net rate of forage uptake during our experiment. Time of day also had a significant effect ( $P < 0.05$ ); on average, the net rate of forage uptake was lower in the afternoon than in the morning hours, probably due to depletion of the standing crop of nectar during the day. Forage type had a significant effect because nectar foragers carried heavier loads than pollen foragers. This agrees with previous reports (Ribbands 1953) and suggests that pollen foragers are limited by storage space on their hind legs rather than by the weight of pollen loads. All foragers but two collected mainly nectar, and we did not detect any consistent switch from pollen to nectar collection or vice versa with foraging experience.

## RESULTS

Individual honey bees gradually increased their mean net rate of forage uptake over the first 7 days of foraging (Fig. 2a). On their first foraging day, the mean ( $\pm$  SE) net rate of forage uptake was only  $0.47 \pm 0.1$  mg/min. This uptake rate gradually increased to about twice the initial rate between days 6 and 10. After day 10, bees gradually decreased their net rate of forage uptake. Note however, that only about a fourth of the foragers had a foraging life span longer than 10 days (unpublished data). Individual bees differed significantly in their rate of increase in the net rate of forage uptake (ANOVA, type III sum of squares,  $F_{16,1555} = 3.6$ ,  $P < 0.0001$  for the effect of foraging experience;  $F_{275,1555} = 2.6$ ,  $P < 0.0001$  for the interaction between individual bees and foraging experience).

In the above statistical analysis, we included all 47 bees, with a range of foraging experience of

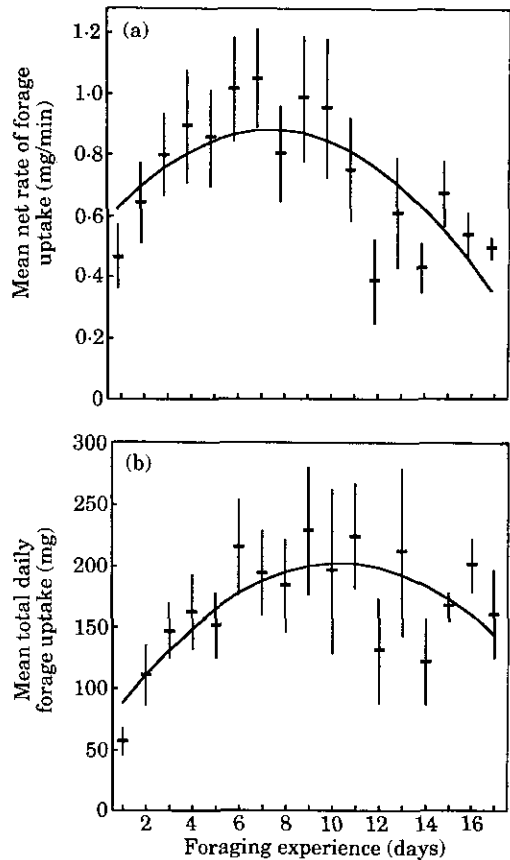
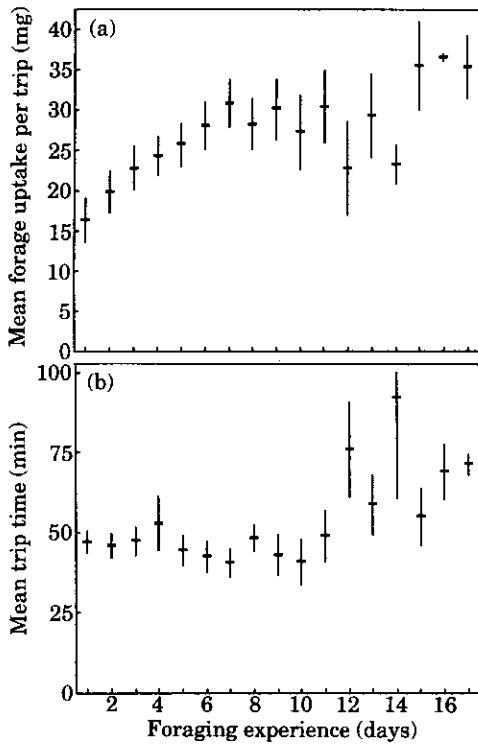


Figure 2. The mean ( $\pm$  SE) net rate of forage uptake (a) and mean total daily forage uptake (b) as a function of the foraging experience of honey bees. The line in each figure depicts a second-order polynomial regression. See Fig. 1 for sample sizes.

2–17 days (Fig. 1). This could have biased our conclusions because we did not compare the same individuals over a given range of foraging experience. Therefore, we repeated our analysis including (1) only the 27 bees that foraged for at least 7 days and (2) analysing only the mean net rate of forage uptake by each bee on each of her first 7 foraging days. The second analysis has the advantage of allowing us to use the more powerful multivariate repeated-measures ANOVA, and the disadvantage of losing a sizeable portion of the original data set. Once again, this analysis showed that both foraging experience and the interaction between individual bees and foraging experience were significant ( $F_{6,49} = 4.4$ ,  $P < 0.001$  for foraging experience;  $F_{156,295} = 1.7$ ,  $P < 0.01$  for

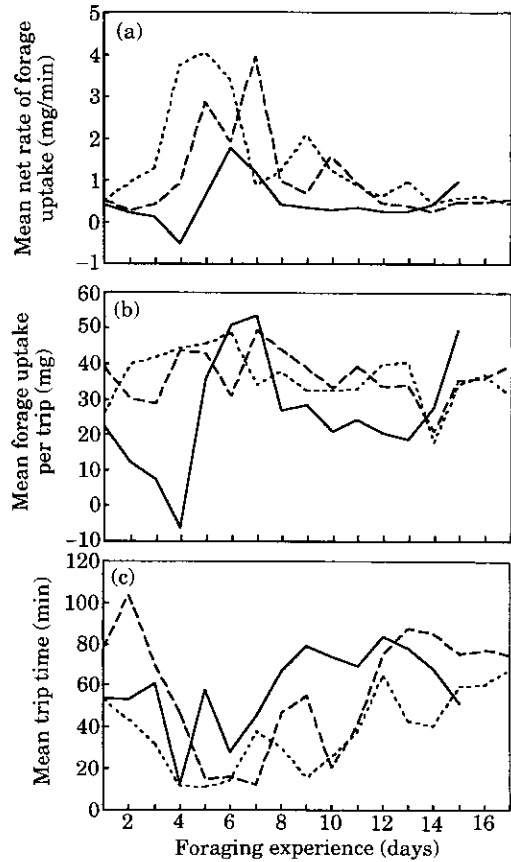


**Figure 3.** The mean forage uptake per trip (a) and mean trip time (b) as a function of the foraging experience of honey bees. See Fig. 1 for sample sizes.

the interaction). An additional analysis of the 27 bees that foraged for at least 7 days showed that 17 bees (63%) had a higher rate of forage uptake on day 7 than on day 2; nine of the 17 bees initiated foraging during the first 9 days of the experiment, and the remaining eight bees started foraging during the second half of the experiment.

The significant increase in net rate of forage uptake also translated into a higher overall forage uptake collected by more experienced foragers ( $F_{16,1555}=4.7$ ,  $P<0.0001$ ; Fig. 2b). In other words, bees doubled their daily contribution to their colony's food supply after a week of foraging experience (multivariate repeated-measures ANOVA for the 27 bees that foraged for 7 days,  $F_{6,49}=2.6$ ,  $P<0.05$ ).

The increase in bees' mean net rate of forage uptake with experience resulted mostly from a two-fold increase in the average weight of forage uptake per trip, and only from a slight and non-significant average decrease in trip time (multivariate repeated-measures ANOVA for the 27



**Figure 4.** The mean net rate of forage uptake (a), mean forage uptake per trip (b) and mean trip time (c) as a function of the foraging experience of three individual honey bees. These three bees had the longest foraging records.

bees that foraged for 7 days,  $F_{6,49}=3.2$ ,  $P<0.01$  for forage weight;  $F_{6,49}=0.7$ ,  $P>0.5$  for trip time). On the other hand, the decrease in mean net rate of forage uptake by older foragers seemed to result mostly from an increase in mean trip time (Fig. 3).

Individual bees varied greatly in all of the above parameters (Fig. 4). However, the general pattern of a gradual increase in mean net rate of forage uptake followed by a decrease still remained for most individuals. For example, one of the three arbitrarily chosen bees depicted in Fig. 4a achieved the highest mean net rate of forage uptake on day 5, and the other two bees peaked on day 6 and day 7, respectively. Overall, 30 (70%) of the 43 bees that foraged for at least 3 days

showed an unambiguous increase in uptake rate during their lifetime.

## DISCUSSION

Individual honey bees gradually increased their foraging performance over a period of more than a week. This period coincided with the bees' mean and median life span as foragers. Therefore, it seems that forager honey bees spend a significant portion of their life span learning and improving in their central task of collecting floral reward. The effect of this prolonged learning on foraging performance disappears only when the longer-lived foragers undergo senescence. Note that our measure for lifetime learning is indirect, and should therefore be strengthened by more controlled studies in the future. Nevertheless, at least one other study presents evidence in agreement with our interpretation of prolonged learning in bees. Schweiger (1958 cited in von Frisch 1967) suggested that more experienced honey bees are more accurate in encoding the distance to a food source in their waggle dances. Cartar (1992) also found an increase in foraging performance of worker bumblebees over a period of 5 days; this suggests that our results may not reflect a unique learning ability of honey bees.

The obvious benefit from long-term learning by bees is a vast increase in foraging performance. This translates into a much higher contribution by experienced bees to their colony's food supply (Fig. 2b). We cannot yet determine whether such long-term learning involves a significant cost. Moreover, we do not even know what exactly the bees learn. Honey bees are known to learn tasks such as flower handling and navigation to and from floral patches. Such tasks, however, may be learned quickly over only several trials (e.g. von Frisch 1967; Menzel et al. 1974; Laverty 1980; Gould & Gould 1988; Seeley & Visscher 1988). Therefore, they are unlikely to explain the apparent long-term learning observed in our experiment. Such long-term learning may reflect more subtle skills that bees learn. For example, bees may gradually improve in their ability to assess when to either switch to known alternative plant species or search for better novel sources. Although honey bees can also gain information about alternative forage through scout dances in the hive, they still have to decide whether to

attend to such information and whether they should switch to a newly advertised food source. Such skill may require a considerable amount of foraging experience. Bees also may learn the best forage available at several locations at different times during the day (Koltermann 1974). It is also possible that bees require a long time to acquire detailed geographical knowledge that enables them to forage on superior but more distant floral sources.

Learning might involve several costs. First, learning new skills usually involves an initial stage when the naive forager is less successful in obtaining food. This may result, for example, from either searching for food in poor sites, or handling the food incorrectly (Laverty 1980; Heinrich 1984). Second, searching for food in unfamiliar sites may increase the risk of death due to either predation or inability to find the way back to the hive. Third, learning new information may interfere with essential information that has already been learned (Stanton 1983; Lewis 1986; Waser 1986; Croy & Hughes 1991). Further experiments are necessary to evaluate both the exact skills bees learn over their life span, and the associated costs.

We interpret the increase in net rate of forage uptake with increased experience (Fig. 2a) as learning. Learning is usually inferred indirectly by an observed change in behaviour (Papaj & Prokopy 1989). We must therefore caution that non-cognitive changes may have contributed to the observed changes as well. However, we do not know of physical or physiological changes unrelated to learning which could lead to increased foraging performance. On the other hand, non-cognitive processes that might be involved in the striking decline of foraging performance with senescence (Fig. 2a) are well known. Such processes may involve either physical wear (Collatz & Wilps 1986), degeneration of the central nervous system (Kern 1986) or both (von Frisch 1967, page 74). One possibility is that bees take higher risks after a few days of foraging, and that this results in a higher rate of forage uptake. This alternative is not supported by the survival data, which do not show an unusual increase in probability of mortality with foraging experience (unpublished data). However, we cannot reject this alternative and intend to evaluate it in a future study.

Our results suggest that even short-lived bees spend a considerable portion of their lifetime

learning. Moreover, it is likely that some of the long-term learning results from a slow acquisition of complex skills which have not been well studied in insects. Much more theoretical and empirical research is needed for a more complete understanding of the lifetime aspects of learning and their relation to fitness. We believe that both our subject animals, short-lived bees, and our natural experimental paradigm are ideal for such further investigation.

### ACKNOWLEDGMENTS

We thank R. Cartar, L. Gass, T. Laverty, T. Seeley, J. Smith, R. Vetter, N. Waser, M. West and an anonymous referee for comments on the research and/or manuscript. This work was supported by NSF grants no. BNS-9009325 to P.K.V. and BSR no. 8905808 to N. M. Waser.

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