Age-related Sampling of Food Sources in Unsuccessful Foraging Bumblebees [Hymenoptera: Apidae: Bombus]

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Naive *Bombus terrestris* (Linnaeus 1758) bumblebees that failed to learn to handle feeders of sucrose solution were examined for sampling frequency and duration until they stopped their feeding attempts. The number of sample-bouts [attempts to feed], the duration of each sample-bout, and the time between subsequent sample-bouts [pauses] were measured. The question was whether the age and cohort of the unsuccessful bees correlated with their feeder-sampling behaviour. Younger bees sampled the feeders more frequently, but stayed a shorter time during each sample-bout, than older bees. The duration of each separate pause was longer for older bees than for younger bees. The total sampling-time before giving up tended to be higher for the older bees. Bee cohort, and colony size at the time of observation, did not affect sampling frequency and duration in the unsuccessful foragers. For all bees, subsequent sample-bouts decreased in duration, while the duration of each subsequent pause increased. This was possibly due to negative reinforcement by the unsuccessful samples. The higher sampling frequency of the younger bees may be considered part of a first orientation and learning process of handling of food sources. The longer durations of sample-bouts and pauses in the older workers may reflect the effects of senescence on foraging behaviour.

Key words: *Bombus terrestris* [Linnaeus 1758] – artificial feeder – cohort - colony size – foraging – handling – motor learning – senescence

קיסר ת, חוביץ ש ושמידע א [מדה"ח, מכללת אחוה]: דגימת מקורות מזון תלוית-גיל בדבורת הבומבוס [Hymenoptera: Apidae: Bombus]
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תקציר

אפיינו את התנהגותן של דבורי בומבוס (Linnaeus 1758) *Bombus terrestris*, אשר לא הצליחו לבצע משימת למידה מוטורית אופרנטית (שתיית תמיסת סוכר מתוך מאכלה) בתנאי מעבדה. מדדנו את מספר הניסיונות הכושלים לבצע את המשימה, את משך הזמן שהוקדש לכל ניסיון, ואת אורך ההפוגות בין ניסיונות עוקבים, עבור פועלות משלוש קבוצות גיל. פועלות צעירות דגמו את המאכלות מספר רב יותר של פעמים מאשר פועלות זקנות, אך משך כל דגימה היה קצר יותר. פועלות זקנות גם ערכו הפוגות ארוכות יותר בין דגימה לדגימה בהשוואה לפועלות צעירות. פרטים זקנים נטו להקדיש זמן ארוך יותר לדגימה, במצטבר, מאשר פרטים צעירים. בכל קבוצות הגיל חלה ירידה במשכי הדגימות, ועליה במשכי ההפוגות, לאורך תקופת התצפית. ההבדלים תלויי-הגיל בתדירות דגימה של מקורות מזון עשויים להעיד על נטייה רבה יותר של פועלות צעירות ללמידת מטלות מוטוריות (כגון טיפול בפרחים בעלי מורפולוגיה מסובכת) בתנאים טבעיים. הפעילות האיטית יותר, שנצפתה בפועלות הזקנות, עשויה לנבוע מבלאי על מערכות השרירים והתנועה בגיל מבוגר.

מילות מפתח: גודל המושבה - דבורת הבומבוס - הזדקנות - טיפול - למידה מוטורית – מאכלה - קבוצת גיל - שיחור מזון

1 Introduction

Bees integrate geographic, olfactory and visual information to find and recognize floral food sources [COLLETT & KELBER 1988, LUNAU 1992, GOULD 1993, CHITTKA, KUNZE & GEIGER 1995, GIURFA, NÚÑEZ, CHITTKA et al 1995, WEHNER, MICHEL & ANTONSON 1996, CHITTKA & RAINE 2006, SALEH, OHASHI, THOMSON et al 2006]. These cues are learned extremely rapidly [MENZEL, GREGGERS & HAMMER 1993]. The identification of food sources involves neural modulations that lead to changes in behaviour [FAHRBACH & ROBINSON 1996, HAMMER 1997]. Another important step in the foraging process, the manipulation and correct handling of flowers, requires learning as well [HEINRICH 1979, LAVERTY 1980, 1994, CHITTKA & THOMSON 1997]. Inexperienced bees make many types of 'errors' on their first flower visits. These errors include landing on inappropriate areas of the flower, assuming incorrect positions, and probing in areas far from the nectar source [HEINRICH 1976, LAVERTY 1980]. Handling performance gradually improves with experience, but this improvement is more time-consuming than the learning of floral display cues [LAVERTY 1994, KEASAR, MOTRO, SHUR et al 1996]. Handling of simple flowers is learned faster than handling of flowers of complex morphology. Specialist pollinators are faster learners of handling techniques, for their specialty, than generalists [LAVERTY & PLOWRIGHT 1988, LAVERTY 1994].

Thus, bees face two types of learning tasks while foraging: sensory discrimination learning that allows them to choose profitable food sources, and motor learning that allows efficient handling of these sources. Considerable variability among individuals exists for both types of tasks [KEASAR et al 1996, BEN-SHAHAR, THOMPSON, HARTZ et al 2000, CHITTKA, DYER, BOCK et al 2003, BURNS 2005, RAINE, INGS, RAMOS-RODRIGUEZ et al 2005]. Some of the correlates of individual variability in sensory discrimination learning have been elucidated. These include genetic differences in perceptive and learning capabilities between bee strains [BENATAR, COBEY & SMITH 1995, PANKIW & PAGE 1999] and between individual foragers [SCHEINER, ERBER & PAGE 1999, RUEPPEL, CHANDRA, PANKIW et al 2006]; trade-offs between discrimination accuracy and foraging speed [CHITTKA et al 2003]; the bees' level of satiation [BEN-SHAHAR & ROBINSON 2001]; the bees' wing wear [HIGGINSON & BARNARD 2004]; and differences in learning capacity between workers of different ages [LALOI, GALLOIS, ROGER et al 2001] or different tasks in a colony [RAY & FERNEYHOUGH 1997, BEN-SHAHAR et al 2000]. Much less is known about motor learning by bees [CHITTKA 1998, 2002], and particularly about the factors that underlie individual variability in performance of motor tasks. Measurements of motor performance in bumblebees challenged with a discrimination task revealed no correlation between an individual's success in the discrimination task and its motor skills [KEASAR et al 1996]. This finding suggests that the efficiency of discrimination learning and of motor learning in bees may be influenced by different genetic and/or environmental factors.

In the present study the focus was on individual variability in learning of motor skills by foraging bumblebees, and it was tested whether forager age correlates with this variability. Task allocation among bumblebee workers (unlike the situation in honeybees) is not strongly age-based, and workers leave the colony to forage at different ages. Moreover, most workers perform both foraging and in-nest tasks throughout their lives [O'DONNELL, REICHARDT & FOSTER 2000]. The null hypothesis was, therefore, that workers of all ages would be similarly adept at learning motor tasks related to foraging, given equal foraging experience. A different hypothesis arises from general learning theory, which predicts that the value of learning for animals is inversely related to their life expectancy. This hypothesis suggests that foragers trade-off time and energy spent on learning new skills with time spent on exploiting familiar food sources. Older foragers (with a relatively low life expectancy) are expected to reduce their investment in learning of new foraging skills, because they have a shorter time horizon ahead of them to exploit the learned information [STADDON 1983, KREBS & KACELNIK 1984, DUKAS & VISSCHER 1994].

According to this 'value of learning' hypothesis, young bees are expected to invest more in learning of a novel motor task than older individuals. The null hypothesis focuses on age-related differences in learning ability, while the 'value of learning' hypothesis stresses age-related differences in the motivation to learn. Thus, the two hypotheses are not true alternatives. Nevertheless, they produce distinct and testable predictions: the 'value of learning' hypothesis predicts age effects on learning performance, while the null hypothesis predicts no such effects.

Previous studies did not find evidence for age effects on the learning of a color-discrimination task by bumblebees that foraged on feeders in a flight room [KEASAR et al 1996, RAINE et al 2005]. Another experiment was conducted to test for age-related differences between bees challenged with a feeder-handling motor task. Two groups of foragers were observed during the experiment, a large group that succeeded in handling the feeders [n = 209] and a group that did not succeed in handling them correctly [n = 20]. The behaviour of each group was examined separately for age-effects. The data of the successful foragers, whose age ranged 1–20 d, offered no indication of age-dependent learning (unpublished results). The present study will therefore report on age-related behavioural differences in the unsuccessful group only.

A sample was defined as an attempt to obtain sucrose from the feeders. The frequency of unsuccessful samples, and the duration of these samples, were used as the behavioural parameters. These parameters were measured in a laboratory setup, with artificial feeders of identical simple morphologies. Effects of colony growth were examined, because the reproductive state of the colony affects worker behaviour [DUCHATEAU & VELTHUIS 1988], and could therefore influence foraging effort. The effect of cohort [colony age] was examined as well, as [CAMERON 1989] showed that successive cohorts forage more intensely.

2   Methods

2.1   Experimental environment

Experimentally naïve workers of *Bombus terrestris* of one colony were allowed to fly freely around a 2x4 m laboratory room. The room was illuminated between 6:30 and 18:30 by six OSRAM F 40 CW 100 Hz white fluorescent lamps. The temperature in the room ranged 27–31 °C, and the relative humidity was 40–85%. Colony size increased from 99 –158 bees during the period of observations. The bumblebees were supplied with pollen into the colony *ad libitum*. Scented sucrose solution [30% w/w concentration] was offered in a petri-dish feeder outside the colony, and was removed 12–15 hour prior to experiments, to motivate the bees to forage. All newly emerged bees were individually marked inside the colony once a week, and thus the age of each bee was known with an uncertainty of 6 days. In-nest marking was conducted at weekly intervals to reduce disturbance to the bees. During observation sessions, the experimenters also looked for unmarked bees that were active in the flight room. These bees may have hidden in the nest as adults during the previous in-nest marking, or may have eclosed from the pupa after the last in-nest marking. These individuals were excluded from the observations, to improve the accuracy of age estimates.

2.2   Feeders

32 identical feeders were placed in a semi-random arrangement on a 140 cm x 160 cm table with a 12x14 position grid. Distances between neighboring feeders did not exceed 15 cm. The morphology of the feeders embodied a round, flat, green or white corolla, with a round opening on the top, in which sucrose solution was visible to the bees [KEASAR 2000: detailed description]. The experimental feeders required a different handling technique from the petri-dish feeders. All feeders contained 1 μl of the 30% scented sucrose solution at the start of each observation session. The feeders were connected to a computer that refilled them according to a probabilistic schedule after they were depleted. Without nectar depletion by the bumblebees, however, nectar was always available and could be detected by olfactory and visual cues. During the experiment bees never depleted the nectar sources, and therefore all feeders were equal in reward to the approaching bees.

2.3 Experimental design

All the bees, regardless of age, had no previous experience in foraging except for the petri-dish feeder, and were therefore naive to the motor foraging task. Some bees never succeeded to actually reach the nectar-source (n = 20). Each bee's first attempt to handle the feeders, and its subsequent unsuccessful sampling events, were observed during a 3-hour period. The time spent continuously on the patch with feeders (including transitions among feeders) was defined as one sample-bout. During a sample-bout the bees could sample one or more feeders. The time from leaving the patch until return- ing was counted as one pause. During a pause bees could fly around, rest in the room or return to the colony. The numbers and the durations of the sample-bouts and pauses were recorded. The number of sample-bouts, and sampling and pausing durations were related to the age of the bees. Because the exact ages of the bees are not known, they were divided into three groups according to their age at the time of observation. Age group one consists of bees 1–10 days old [n = 6], age group two of bees 11–20 d old [n = 9], and age group three consists of bees 21–30 d old [n = 5]. The number of sample bouts was the only dependent variable that deviated from normal distribution. The effect of age group on the number of sample-bouts was therefore analyzed with a Kruskal-Wallis tied-rank test. This test was followed by a non-parametric multiple-comparison test of the Student-Newman-Keuls type for unequal sample sizes with tied ranks [Zar 1996]. Sampling and pausing durations were analyzed for age-effects using one-way ANOVAs, followed by Duncan ranking tests. The effect of colony age (bees marked in the same calendar week were defined as one cohort), and of the number of bees in the colony on the behavioural parameters, were examined.

3 Results

3.1 Age effects

Older bees made fewer sample-bouts than young bees (Fig 1). The difference in the number of sample-bouts between age groups 1 and 3 was marginally significant [Q = 2.52, p = 0.05, Kruskal-Wallis test followed by Student-Newman-Keuls multiple comparisons]. Younger bees returned to try to handle the feeders more often than older bees. The mean total time [±SE] spent sampling the feeders, during all sample-bouts combined, was highest for age group 3 [n = 5, 510.0±42.5 s] and lowest for age group 1 [n = 6, 280.8±10.4 s]. These differences were not statistically significant, however. Thus, older bees may have tried to handle the feeders only once or twice, but the durations of these trials were longer (Fig 2). The durations of the first sample-bout differed significantly among age groups 1, 2 and 3 [one-way ANOVA followed by Duncan ranking tests, $F_{18,2}$=86.47, P = 0.0001]. The durations of the second sample-bout were significantly longer for age group 3 than for the younger bees [ANOVA followed by Duncan ranking tests, $F_{18,2}$ = 1.11, P = 0.005]. The duration of the third sample-bout was not significantly affected by age group [$F_{13,2}$ = 8.91, P = 0.31].

Bees of age group 3 also spent more time off the patch of feeders between subsequent sample-bouts, as compared to bees of age group 1 (Fig 3).

The mean total time [±SE] spent off the patch, during all pauses combined, was 434.68±47.4 s for age group 3 and 337.0±64.2 s for age group 1. The duration of the first pause did not differ significantly between age groups 1 and 2, but both groups differed significantly from group 3 (ANOVA followed by Duncan ranking tests, $F_{18,2}$ = 13.85, P = 0.0001). The duration of the second pause was significantly different between age groups 1 and 2 (ANOVA followed by Duncan ranking tests, $F_{13,2}$ = 127.4, P = 0.0001).
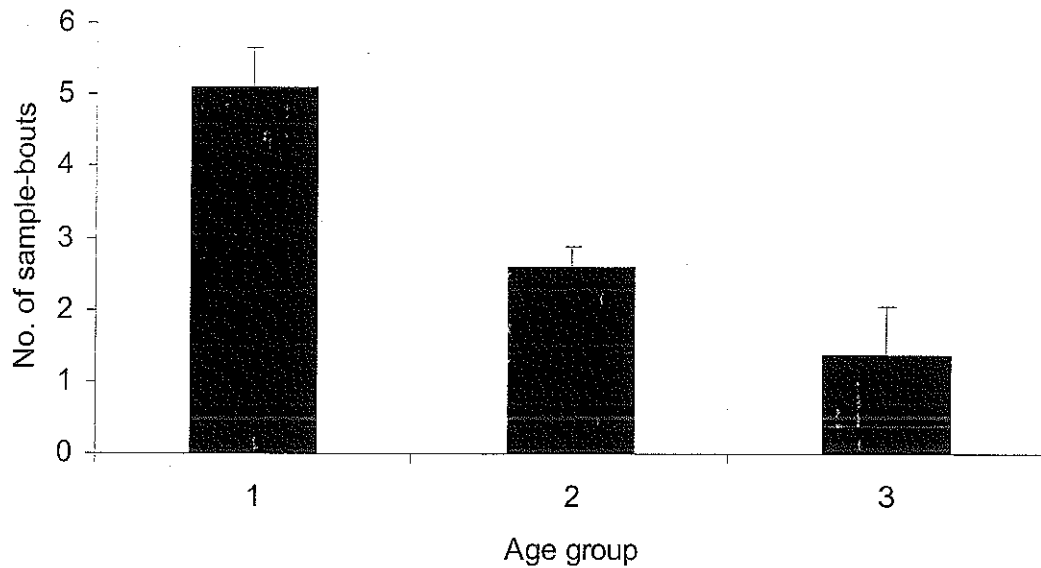
Fig 1: The average number of sample-bouts per age group recorded during a three-hour observation period of each bee (Hymenoptera: Apidae: *Bombus terrestris* Linnaeus 1758). – Error bars are 1 SE. Bees in age group 1, 2 and 3 are 1–10 [n = 6 bees], 11–20 [n = 9] and 21–30 [n = 5] days old, respectively.

3.2 Variation between the sample-bouts

In addition to the variation among age groups in the durations of sample-bouts, variations among subsequent sample-bouts within bees of the same age group were also observed. For each age group, the duration of the sample-bout decreased for each subsequent bout. This trend was significant for age group 1 [$F_{29,5}$ = 28.92, P = 0.001], age group 2 [$F_{26,2}$ = 53.98, P = 0.001] and age group 3 [$F_{17,1}$ = 10.28, P = 0.02]. Post-hoc comparisons indicated that subsequent sample-bouts differed significantly in duration in most cases, with the exception of sample-bouts 4–6 of age group 1 (**Fig 2**). At the same time, the time spent off the patch for age groups 1 and 2 increased for each subsequent pause. For both age group 1 and 2, pauses 1 and 2 differed significantly in duration from each other (**Fig 3**). In other words, the bees attempted to feed from the feeders for a shorter time in consecutive sample-bouts, and stayed away longer.

3.3 Effects of colony development and cohort

The typical growth of bumblebee colonies follows a sigmoid function and is affected by two marked reproductive events: the onset of male production by the queen, and the onset of worker reproduction [DUCHATEAU & VELTHUIS 1988, GOULSON 2003]. During the period of observation the colony grew at a constant rate from 99 to 158 female workers, with the queen always present. No young queens emerged during the period of observations. Therefore all the observations probably took place at the same stage of colony development, so that no major effects of colony-level endocrine changes on worker behaviour are expected.

No effect of the week of eclosion on the sampling behaviour of unsuccessful foragers was found.
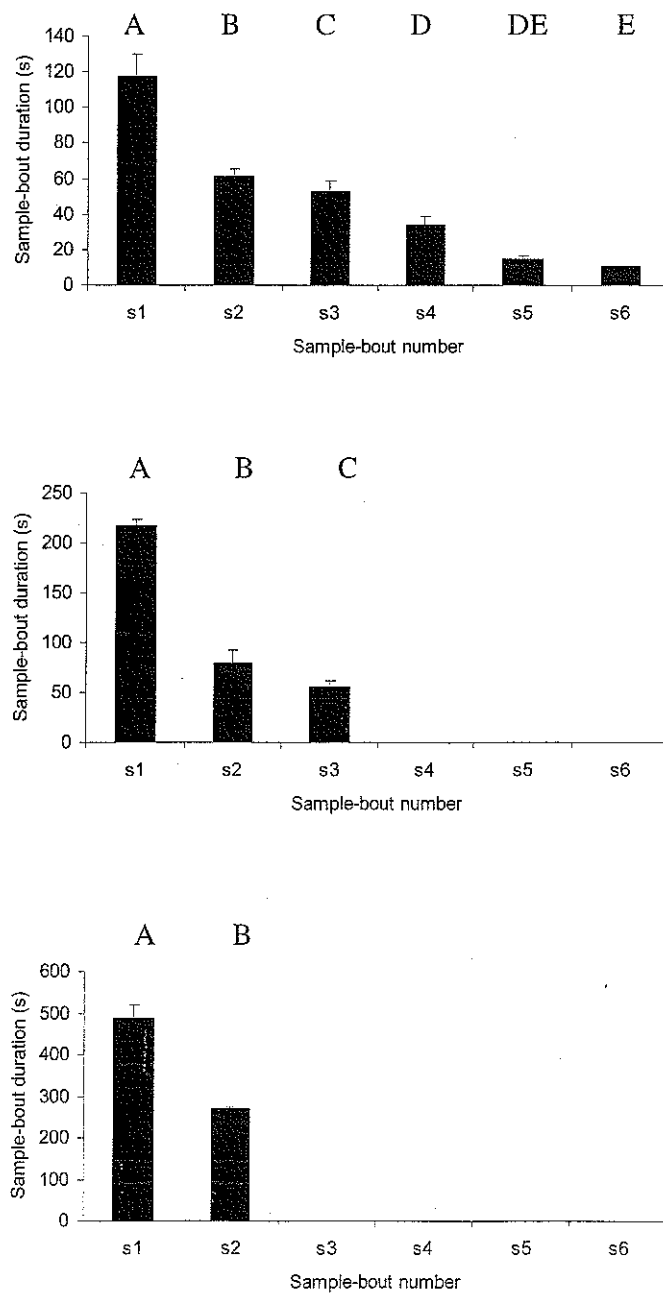
Fig 2: Mean durations of subsequent sample-bouts of bees (Hymenoptera: Apidae: *Bombus terrestris* Linnaeus 1758) in age group 1 (top), 2 (middle) and 3 (bottom). – Error bars are 1 SE. Columns marked by the same letter were assigned into one group by Duncan post-hoc ranking tests.
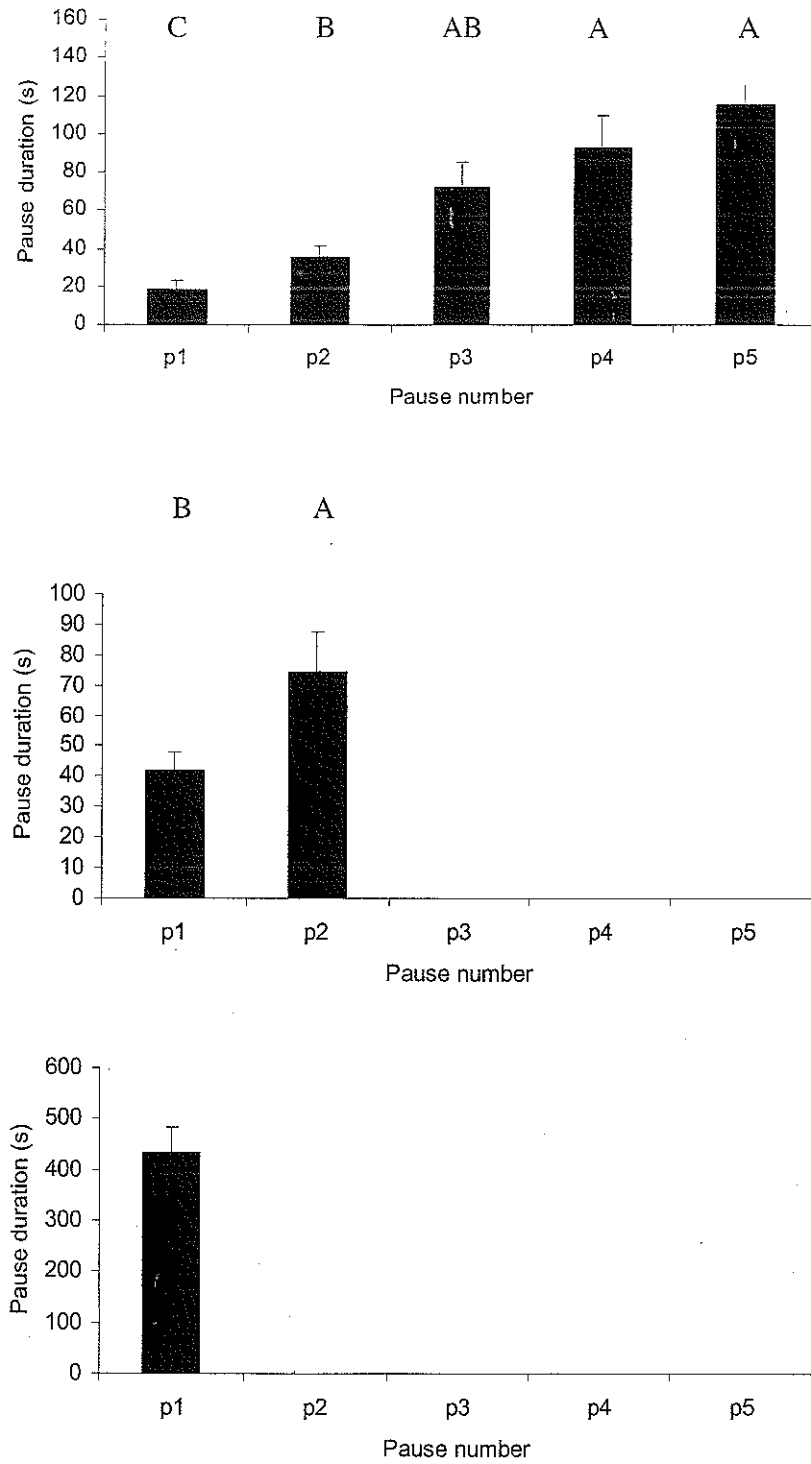
Fig 3: Mean durations of subsequent pauses of bees (Hymenoptera: Apidae: *Bombus terrestris* Linnaeus 1758) in age group 1 (top), 2 (middle) and 3 (bottom). – Error bars are 1 SE. Columns marked by the same letter were assigned into one group by Duncan post-hoc ranking tests.

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Bees of one cohort (emerged within the same week of colony life) foraged at different ages. This variability allowed us to compare the number of sampling-bouts, pauses, and their durations, among cohort-mates that differed in age at their first foraging attempt. This is exemplified for bees of cohort 2 that sampled the feeders both in age group 1 and in age group 2. The number of sample-bouts is lower for the higher age group, the duration of the first sample-bout is longer for the higher age group and so is the duration of the first pause [Tab 1]. Bees of the same age in different cohorts, on the other hand, exhibited similar numbers and durations of sampling-bouts and pauses. The behavioural patterns in trying to handle the feeders are therefore related to differences in age.

Tab 1: Behavioural parameters for bees (Hymenoptera: Apidae: *Bombus terrestris* Linnaeus 1758) of cohort 2 in age group 1, and other bees of the same cohort that were observed when they reached age group 2. Mean values (± standard errors) for the number of sample-bouts, the duration of the first sample-bout and the duration of the first pause are provided.

Age group	Number of sample-bouts	Duration sample-bout 1 [s]	Duration pause 1[s]
1 [n = 4]	5.0±0.4	103.8±9.2	20.0±5.4
2 [n = 2]	3.0±0.0	235.0±15.0	52.5±7.5

4 Discussion

The observations indicate age-related differences in the unsuccessful attempts of *B terrestris* workers to complete an operant motor task. Success itself was not related to age, since the unsuccessful group (aged 1–25 d, described here) and the successful workers (aged 1–20 d, unpublished data) had similar age ranges. Unpublished data on the age distribution of foragers from a large number of experiments in our laboratory indicate that age groups 1, 2 and 3 together account for 91.9% of all foraging bees. While the longevity of non-foraging *B terrestris* workers is about two months, foraging bumblebees usually survive only two weeks in the field [GOLDBLATT & FELL 1987, SMEETS & DUCHATEAU 2003]. Survival of foragers under laboratory conditions is likely to be somewhat higher than in the field, because they do not suffer predation. Thus, estimates of forager life expectancy agree with the age of the oldest foragers observed in the present study.

The null hypothesis predicted no effects of forager age on flower handling behavior. This prediction is not supported by the data. As predicted by the 'value of learning' hypothesis, younger bees tried to handle the feeders more often than older bees. The 'value of learning' hypothesis does not fully explain the results reported here, however, because young bees did not spend more time trying to learn the task than older bees. On the contrary, older bees spent more time sampling the feeders than younger bees, both in each sample-bout and when the total sampling time was considered. In general, the older bees tried to handle the feeders only once or twice, and stayed a long time in the patch during this effort. This could be an effect of senescence, as honeybees become less efficient foragers with age [THOMSON, MADISON & PLOWRIGHT 1982, DUKAS & VISSCHER 1994, TOFILSKI 2000]. Bumblebees also become less efficient foragers with age, and are less likely to explore new plant species, even with greater reward [HEINRICH 1979].

The sluggish foraging of the older bees may act as a physiological limitation to efficient learning of motor skills. Alternatively, the greater persistence of the older foragers could be interpreted as an adaptive behavior that may increase their probability to ultimately learn the motor task. It is therefore not possible to predict the fitness consequences of the observed age-related differences for foragers under natural conditions.

Interestingly, significant age-effects were observed for the small group of unsuccessful bees, but could not be detected in the much larger group that succeeded in learning the motor task. A possible reason is that mean feeder handling durations were two orders of magnitude shorter for the successful foragers [e.g KEASAR et al 1996] as compared with the unsuccessful ones. Differences between age groups may be harder to detect when handling durations are so short.

The results show a decrease in the duration of subsequent sample-bouts for all age groups, and an increase in the duration of subsequent pauses in age groups 1 and 2. Age group 3 could not be analyzed for the durations of subsequent pauses, because only a single pause was recorded for this age group. The decreasing durations of sample-bouts, and increasing pause durations, suggest that the unsuccessful samples of feeders are a negative reinforcement to the subsequent samples. Such negative reinforcement may result in a longer time before trying again. Under natural conditions bees may use this time to explore the area for other flower types, rather than repeatedly attempt a non-rewarding food source. Thus, the bees' recurrent sampling of the feeders may, to some extent, reflect the limitations of the experimental design.

Previous studies documented an increase in the foraging efficiency of bees, over the course of several consecutive days [DUKAS & VISSCHER 1994, KEASAR et al 1996]. In these studies, the effects of forager age and experience could not be teased apart, since the experimental subjects became both older and more experienced as the experiment progressed. The present study takes a complementary approach, by comparing the behaviour of bees of different ages but with the similar foraging experience. The results may relate to previous evidence for a limited degree of age-related division of labor in bumblebees. Older bumblebee workers are more likely to perform foraging tasks than younger bees, and foragers switch from nectar to pollen collection as they age [reviewed by GOULSON 2003]. The age-based polyethism in bumblebees is much more flexible than in honeybees, however, and does not seem to involve age-related differences in sensory discrimination learning abilities [KEASAR et al 1996, RAINE et al 2005]. The findings reported here provide a first hint to possible age effects on the motor learning capabilities of bumblebees.

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PENEA J E, SHARP J L & WYSOKI M (Eds): **Tropical Fruit Pests and Pollinators**. Biology, Economics, Importance, Natural Enemies and Control. – [VIII+430 pag, 9 fig, 16 col plat, 22 tab, 170 x 245 mm, balacr.hardcov]. – **Publ:** CABI Publishing, Wallingford/UK; **ISBN:** 0-85199-434-2; **Pr:** Brit £ 95,00.   – – –   [EGR-Nr 3.034]

Insect pests cause major economic damage on fruit crops in the tropics. However, some insects are beneficial and have a role in pollinating flowers, thus enabling fruit set. This book, written by leading authors from around the world, reviews the harmful as well as the beneficial insects, and how they might be controlled to enhance fruit production and quality. The contents include the following chapters: (1) PEÑA J E: Introduction. (2) GOLD C S, PINESE B & PEÑA J E: Pests on Banana. (3) Smith D & PEÑA J E: Tropical Citrus Pests. (4) Waite G K: Pests and pollinators of Mango. (5) PANTOJA A, FOLLETT P A & VILLANUEVA-JIMÉNEZ: Pests of Papaya. (6) PETTY G J, STIRLING G R & BARTHOLOMEW D P: Pests of Pineapple. (7) PEÑA J E, NADEL H, BARBOSA-PEREIRA M & SMITH D: Pollinators and Pests of Annona Species. (8) WYSOKI M, VAN DEN BERG M A, ISH-AM G, GAZIT S PEÑA J E, PEÑA J E & WHITE G K: Pests and Pollinators of Avocado.

(9) GOULD W P & RAGA A: Pests of Guava. OOI P A C, WINOTAI A & PEÑA J E: Pests of Minor Tropical Fruits. (11) WAITE G K & HWANG J S: Pests of Litchi and Longan. (12) AGUIAR-MENEZES

E L, MENEZES E B, CASSINO P C R & SOARES M A: Passion Fruit. (13) SHARP J L & HEATHER N W: Quarantine Treatments for Pests and Tropical Fruits.

With concern to the major theme of this journal issue, there are three chapters dealing with pollinators: (**a**) Pollination in mangoes might be mediated by insects rather than wind, dependent on region and environment. There seems to be a consensus that numerous species within the complex of visiting insects contribute to the pollination of flowers. Diptera, mostly Calliphoridae and Syrphidae, are the most common visitors in Costa Rica and India. Hymenoptera were found more prevalent in terms of species in Australia and South Africa. Experiments conducted in Northern Australia showed that wasps and native bees (*Trigona* species) were more effective pollinators than were large flies. *Trigona* species are suggested to become used to augment the pollinating fauna, since they are common in Northern Australia, prevalent on mango blossom and can be hived – whereas mango flowers are generally considered to be unattractive to the naturally uncommon *Apis mellifera*. *Trigona* species are also associated with mangoes in Costa Rica, but appear to be unimportant as pollinators. In Thailand, however, the locally common honeybee species *Apis cerana* is preferred for small honey production and for pollinating mangoes. In India, studies are conducted to develop in-tree rearing of flies (Calliphoridae: *Lucilia*, Sarcophagidae: *Sarcophaga*) that woud assist in mango pollination.

(**b**) The guilds of pollinating Coleoptera (Nitidulidae, Cucujidae, Staphylinidae, Scarabaeidae) and Hemiptera (Anthocoridae) in commercial Annona species (*Atemoya, Cherimoya*) vary geographically, and species may even perform differently in each area. The four major pollinators in Israel (*Carpophilus humeralis, C hemipterus, C mutilatus, Harpactonus luteolus*) are equally effective in Florida. In Florida, about nine species of native and exotic Nitidulidae visit the flowers, but *C mutilatus* is the most important pollinator in terms of efficacy and abundance in flowers, followed by *C fumatus* and *H luteolus*. Although *C humeralis* is very abundant in the annona grove environment, it rarely visits the flowers. When it does visit, it induces a very low rate of fruit set, in contrast with its behaviour in Israel. The number of species visiting flowers in Ecuador, Colombia and the Carribean region is similar to that found in Florida. In others the guilds are smaller, and in some cases inadequate for commercial fruit production without the aid of manual pollination. In Costa Rica, the flowers of soursop (*Annona muricata*) attract the beetles one day before the male phase at about 18.oo-22.oo h, when they emit a strong odour. Pollen is transported by Scarabaeidae: (*Cyclocephala* sp) on leg and body hairs. They remain in the flowers for 24 h and leave after the pollen is shed.

(**c**) The flowers of avocado (*Persea americana*) open twice, first as a female and then as a male (*diurnally synchronous dichogamous protogyny, with intermediate closing*). Therefore, pollinators have to visit both female and male stage flowers, and come into contact with the dehisced anthers and the respective stigma at the same hairy pollen collection zones. The avocado flower presents typical generalist features, including large amounts of exposed nectar and pollen. Thus, its rewards are readily available to almost all visitors, from bees, wasps, ants, and flies to beetles, bugs and butterflies. The main original avocado pollinators apparently are social Hymenoptera which co-evolved with avocado for million of years in Central America: several small to medium size stingless bees (Meliponinae) and the Mexican honeywasp, *Brachygastra mellifica*. Numerous species of wasps and flies, and probably also beetles, are second-order pollinators. The arrival of the European honeybee in Central America and the modern agricultural techniques, especially spraying with potent insecticides, changed the ecological conditions there. The honeybee became the major pollinator of many plant species, including avocado, and the original pollinators were excluded into the reduced uncultivated areas. Over the last two centuries, the avocado has been exported from its region of origin to most tropical and subtropical regions of the world. Since its original pollinator species were never transferred to the new growing regions, it is pollinated there by local species. While in most New Worlds tropics there are local stingless bee and wasp species which are evolutionarily related to avocado's original pollinators and may pollinate it effectively, in subtropical countries there are almost no suitable local candidate pollinator species, except for the honeybee.

These reports about pollination in tropical and subtropical fruit plants offer a basis for more experimental studies: a wide field for those who are fascinated to discover the relations of insect sensory systems and behaviour on one hand and their coevolution with flower features on the other.   AWS