Risk-indifferent foraging behaviour in honeybees

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(Received 5 July 1999; initial acceptance 2 September 1999; final acceptance 22 May 2000; MS. number: 6277R)

We studied the influence of variance in reward volume on choice behaviour of honeybees, *Apis mellifera carnica*, by training bees to collect sucrose solution from four newly developed artificial feeders. The feeders were electromechanical devices, each controlled by a microprocessor, which monitored the experiments, controlled reward delivery and stored the data. The parameters that varied between the feeders were the amount and variance of reward. The four feeders were arranged in two pairs, with the two feeders in each pair set to the same reward parameters. Constant feeders offered a fixed amount of sucrose solution at each bee visit; variable feeders offered a normally distributed reward with a standard deviation equal to the mean. We tested three reward combinations under two variance conditions. The bees matched their choice frequencies to the mean amount of reward. This applied both to the constant and the variable feeders. Thus the bees were able to discriminate feeders by the amount of reward and were able to estimate the mean reward for the variable flowers. The proportion of immediate returns to the same feeder increased with the amount of sucrose solution imbibed at each visit, indicating that bees were able to perceive the amount of reward at each visit. However, there was no influence of variance on the choice behaviour of the bees, ruling out the possibility that bees are risk sensitive under these conditions. We discuss risk indifference in choice behaviour of bees in the context of several models of risk sensitivity.

Risk-sensitive foraging has been one of the main topics of foraging theory. Risk in this context refers to the uncertainty of an appetitive variable controlling behaviour during foraging, not to the risk of predation. Since in nature a foraging animal encounters a stochastic world, it should take into account the statistical properties of important stimuli, for example food availability. Foraging animals react not only to the amount of energy obtained, the handling times invested, the rate of encounter and spatial distribution of the rewards, but also to the variances of these parameters (Pyke 1984). An animal can show three behaviours when confronted with variance: (1) risk proneness: when the means are equal the animal prefers the high-variance alternative over the less variable one; (2) risk aversion: when the means are equal the animal prefers the alternative with the smaller variance; (3) risk indifference: the animal ignores the variance (Stephens & Krebs 1986). The most common explanation for risk-sensitive behaviour is a nonlinear relationship between reward gained and the fitness obtained from this reward. Such a function is called a utility function (Stephens & Krebs 1986). If this relationship is a negatively accelerated one (following the law of diminishing returns), the animal should be risk averse, since the amount of fitness gained with a positive deviation from the mean is less than that lost with an identical negative deviation from the mean. Thus mean fitness gained is lower for the more variable alternative. This behaviour is known as Jensen’s inequality rule. The opposite is true with a positively accelerated utility function: in this case the animal should be risk prone. Following the same line of reasoning, risk indifference should occur if the utility function is linear.

Although most studies on risk sensitivity in foraging insects have been on social hymenoptera (honeybees, *Apis mellifera*, bumblebees, *Bombus* spp.), these animals may represent a rather special case. They store food in a manner that reduces the risk of energetic shortfall for each individual, and so the individual forager’s working conditions may differ from those of animals that forage independently. Furthermore, honeybees communicate the location of food resources to each other (von Frisch 1967). These factors should reduce the applicability of shortfall models for social insects (Banschbach & Waddington 1994; Ydenberg & Schmid-Hempel 1994).

Conditions in the colony (food storage, brood, overall size) may also influence the foraging strategy of the individual animal, and thus its sensitivity to risk. Carter &
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Dill (1990), for example, depleted or filled the honey stores of bumblebees and reported a tendency to more risk-prone or risk-averse choice behaviour, respectively. Indeed, data on risk sensitivity in honeybees and bumblebees are rather controversial, which might reflect effects of colony conditions, but also methodological and conceptual problems. To investigate risk sensitivity in honeybees, we used a novel, fully computerized test procedure, and did the experiments during the autumn, when the colony has established a substantial food store, when brood care has dropped to a low level, and when the natural food supply from flowers is scarce.

Risk aversion was shown by Real (1981), Real et al. (1982) and Waddington et al. (1981) in free-flying bumblebees foraging on artificial flowers offering variable and constant rewards. Harder & Real (1987) interpreted these results, assuming that bees optimize the mean rate of reward per flower. Taking travel times into account, they proposed a function that showed a negatively accelerated relationship between the volume of nectar in the flowers and the energy gained. However, the variance of reward per flower. Taking travel times into account, they proposed a function that showed a negatively accelerated relationship between the volume of nectar in the flowers and the energy gained. However, the variance in these studies (Real 1981; Real et al. 1982) was created with feeders that were either empty or filled with diluted honey. Since bumblebees can smell honey from a distance (Marden 1984) they might have been able to avoid the empty flowers without evaluating the existing variance. Furthermore, the authors did not work with individuals marked bees and so lacked control over which bees contributed to which data. Waddington et al. (1981) tackled the same problem and showed that bumblebees given a choice between constant and variable rewards preferred the constant alternative. In their experiments, however, the differences in energetic gain between constant and variable feeders were too low to be recognized by bees (Waddington 1995).

The approaches referred to so far are based on two basic assumptions of optimal foraging theory, namely (1) that the animal maximizes fitness and (2) that it has a perfect knowledge of the world. The first assumption implies, with respect to proximate mechanisms, objective book keeping of energy intake and expenditure while foraging. However, experimental evidence for bees contradicts this assumption. Waddington (1985) showed that honeybees underestimate gains compared to costs, and Waddington & Gottlieb (1990) demonstrated that the perception of food source’s profitability is a nonlinear function of actual rates of net energy gain, and may resemble the Weber–Fechner law of perception (Real 1991; Perez & Waddington 1996), a conclusion also drawn from data on bird foraging by Kacelnik & Brito e Abreu (1998). Furthermore, Balderrama & Núñez (1992) found that metabolic rate does not clearly depend on the load carried by honeybee foragers; rather, it increases with the flow rate of reward experienced at the food source (Moffat & Núñez 1997), indicating that energy consumption depends on the expected reward and thus on the motivational state of the bees at a particular time during their foraging cycle. In addition, Waddington (1990) showed that active regulation of thoracic temperature results in a partial correlation between gains and costs in honeybees. Varjú & Núñez (1991) studied which parameters honeybees optimize. On the basis of experiments by Núñez (1966, 1982), they found that within a range of sucrose flow rates honeybees trade optimizing net energy gain for information. This conclusion was drawn from experiments showing a dependence of crop filling on sucrose flow rate (Núñez 1982). Under certain instances bees return to the hive with a partially filled crop. Although other interpretations have been proposed for this behaviour (Schmid-Hempel 1993), Varjú & Núñez (1993) showed that energy balance models fail to explain their observations.

Together, these findings make it unlikely that bees optimize energy gain. Thus the role of optimization of energy gain in foraging bees might have been overestimated. Such a bias may be due to the general idea of fitness maximization on which evolutionary adaptation theory is based, and may have neglected the constraints under which the relevant data are sampled by the system.

The second assumption referred to above, namely, perfect knowledge of the environment is also questionable. Greggers & Menzel (1993) have shown that a bee foraging in a patch of four artificial flowers learns continuously about the reward conditions of each flower, but does not develop a perfect, stable knowledge of this environment. Both excitatory and inhibitory learning contribute to memory formation, but they do so asymmetrically. To model the bees’ choice behaviour Greggers & Menzel (1993) used the Rescorla–Wagner version of the difference rule (Rescorla & Wagner 1972). They found the best fit with these data if they assumed a positive learning rate of 0.8 and a negative learning rate of 0.08. From these results one would expect risk-prone behaviour in honeybees, because the variable flowers sometimes offering higher rewards should be learned better than the constant ones where there is no deviation from the expected reward.

All these arguments point to a more complex relationship between variance in reward and choice behaviour in honeybees than currently assumed. Therefore, it is not surprising that more recent data give no indication of risk-averse behaviour in free-flying honeybees confronted with variance in sucrose solution concentration (Banschbach & Waddington 1994), or in bumblebees confronted with variance in either sucrose concentration (Waddington 1995) or volume (D. E. Taneyhill, personal communication). In harnessed honeybees, Shafir et al. (1999) found a risk-averse response distribution, but not if zero rewards were avoided. It is thus worth testing more rigorously and with a better experimental design whether honeybees are sensitive to reward variance. We analysed the responses of honeybees to variance in the expected reward. In particular we investigated which strategy bees adopt when they are allowed to adjust their choice behaviour to the actual reward volumes and variances. Thus we studied risk sensitivity in animals that were already familiar with their foraging resources and we present evidence for risk-indifferent choice behaviour.

METHODS

We conducted experiments in the late summers of 1993 and 1994 in the yard of the Neurobiology Institute of the
Free University of Berlin from 0900 to 2000 hours. The outdoor location was chosen to obtain natural conditions. We used 11 free-flying honeybees, *A. m. carnica*, from an outdoor hive, ca. 70 m away. The hive’s honey stores were well filled and had not been manipulated in any way.

**Apparatus**

Individually marked bees were trained to forage on an arrangement of four artificial feeders arranged in two pairs. Figure 1 shows one of the feeders. Bees licked the sucrose solution (35% by weight) from the tip of a brass rod (henceforth called ‘lever’, FL) which was moved in and out of reach of the bee’s proboscis by means of an eccentric cam (EX) driven by an electric motor (EM). In the resting (bottom) position the tip of the lever dipped into a tray with sucrose solution (ST). In the feeding (top) position the bee could reach the tip of the lever with its proboscis and lick the sucrose solution from it. The tip of the lever was covered by a sleeve of fine wire mesh to increase the volume of sucrose solution adhering to it. The bee entered a box at EN and was guided along a short tube to a small hole (0.6 mm) through which its proboscis could reach the lever in its upper position. The entrance of the box was monitored by an infrared photoelectric barrier (ID). For precise determination of the onset of licking, the contact between the bee’s proboscis and the sucrose solution on the lever was measured with a 200-kHz oscillator and a frequency sensor. The sensor’s output was monitored every 10 ms. We observed no aversive reaction by the bees. Thus, on- and offset of licking were precisely monitored and we could control licking time by moving the lever out of reach of the proboscis at any time. As we show below (Fig. 3 in the Results) licking time is a direct measure of the volume of sucrose solution the bee imbibes. Each feeder was controlled and monitored by a microprocessor which was programmed such that the feeders could provide (1) a fixed reward of given duration at every visit (constant reward) and (2) approximately normally distributed reward durations with given mean and variance. Although this design allowed for no delay between rewards, for the reasons described below we introduced a delay of 4 s between rewards at the same feeder.

We recorded the following parameters for each visit of the experimental bee (with an accuracy of 10 ms): (1) entry time: the time at which the bee crossed the photoelectric barrier at the entrance box; (2) licking time: duration of contact of the proboscis with the lever; (3) time between entry and first proboscis contact; (4) time between last proboscis contact and exit of the bee; (5) handling time: the total time the bee spent in the feeder; and (6) maximum lick time available to the bee on a particular visit: time during which the reward was available to the bee. From these parameters we derived: (1) the sequence of visits, (2) the flight time between feeders and (3) the mean and variance experienced by the bee (which

![Figure 1. Schematic drawing of the artificial feeders used in the experiments. (a) Side, (b) top and (c) front views. The bee entered the feeder through the entrance (EN, arrow). This was detected by a photoelectric barrier (ID in b), and the feeding lever (FL) was moved upwards (dashed line in a). The bee inserted its proboscis (PR) through a small hole (H) and licked sucrose solution from the lever. After licking time expired, the lever was moved downwards. In the resting position the lever tip dipped into a tray with sucrose solution (ST in b); (d) and (e) show how the lever was moved up and down. DR: drawer; EM: electric motor; EX: eccentric cam; IR: infrared diode; LP: landing platform.](image-url)
may differ from the one offered since the bee could choose not to collect all sucrose solution offered, thereby altering the mean and/or variance experienced. The end of each foraging bout was recorded by the experimenter.

We chose this design mainly for two reasons: (1) technically speaking, it is relatively easy to control short durations but hard to control small volumes; and (2) it allowed us, at some visits, to offer zero reward, avoiding any possibilities that the bees were able to recognize the state of the feeder visually or by smelling from a distance before probing. Furthermore, any contact of the bee’s proboscis with sucrose could be avoided for nonrewarded visits.

Calibration

Since we controlled licking times, but were interested in the amount of sucrose solution ingested, we needed to determine the function relating volume to licking time. For calibration, we trained a single, marked bee to collect 35% (by weight) sucrose solution from a single feeder offering a constant reward at each visit. The bee was weighed upon arrival and departure from the feeder, so that its weight gain from each feeder visit could be calculated. We did not measure weight gain after each feeder visit, but let the bee visit the feeder often enough to gain ca. 10–20 mg, since the standard deviation of the balance used was ±1 mg. The bees were weighed after licking times of 0.1, 0.25, 0.5, 1.0, 2.0 and 2.5 s, respectively.

Experimental Procedure

We first trained bees to collect 10% sucrose solution (by weight) from a standard pneumatic Plexiglas feeder (von Frisch 1967). One of these bees was individually marked with white paint (water-based “Tipex”) and served as the experimental subject for one experiment. Only one bee was present in the set-up at a time. We trained the experimental bee to use the feeders by first offering a droplet of sucrose solution near the hole inside the entry chamber. After the droplet was deposed, the bee usually started searching inside the chamber and quickly found the hole leading to the lever. Once the bee had learned the location of the reward, it was given ca. 30 rewarded visits during one foraging bout to become accustomed to the devices and to learn to visit all four feeders. The rewards offered during this initial phase were the same as in the following experiment. Once the bee was accustomed to the feeders, it arrived from the hive, foraged on the feeders until its crop was full and returned to the hive (foraging bout). In between bouts the bee stayed in the hive for several minutes.

We placed four feeders on two adjacent, green tables, each measuring 68 × 150 cm and 80 cm high, forming an area of 136 × 150 cm. The tables were positioned under a UV-transparent Plexiglas roof. The feeders were placed at the corners of an imaginary square with a side length of 1.2 m. Diagonally opposed feeders offered exactly the same reward combinations. Thus in each experiment there were two reward conditions, each presented by two feeders. This arrangement combines aspects of the common practice of using either two alternative feeders or several feeders of two types. For technical reasons, we could not use a large number of feeders, but wanted to avoid using only two of them. With two feeders, if the bee leaves the currently visited flower it has only one alternative to choose from. First, it sees only the opposite feeder, not the one on which it is sitting and, second, the already visited feeder will not provide a reward if visited too quickly (unrewarded immediate revisits, see above).

Each experimental bee was tested in three reward volume combinations: (1) two feeders with a 0.5-s reward/visit and two feeders with a 2.5-s reward/visit (notation: 0.5 s/2.5 s); (2) 1.0 s/2.0 s; (3) 1.5 s/1.5 s. These combinations ensured a constant overall (patch) reward for all experiments of 6 s. For each of these reward combinations, each reward was tested alternately in two variance states: constant (C) and variable (V). Each bee was tested with 1.5 s/1.5 s on the first, 1.0 s/2.0 s on the second and 0.5 s/2.5 s on the last day. Each experiment consisted of three phases, which means that the bee first foraged (first phase) at two feeders each providing for example a 0.5-s constant reward and the other two feeders each providing a 2.5-s constant reward/visit. Then the bee foraged (second phase) at two feeders providing a 0.5-s variable reward/visit and two feeders providing a 2.5-s constant reward. Finally, in the third phase two feeders provided a 0.5-s constant reward/visit and the other two a 2.5-s variable reward/visit. Thus a sample experiment would have looked like this: phase 1: 0.5 s C/2.5 s C; phase 2: 0.5 s V/2.5 s C; phase 3: 0.5 s C/2.5 s V (Fig. 2). The constant feeders offered the adjusted reward (0.5, 1.0, 1.5, 2.0, 2.5 s) at each visit, and the variable feeders offered a normally distributed reward time per visit with the mean equaling the indicated reward time. The standard deviation of these feeders always equalled the mean. The other two reward combinations besides 1.5 s versus 1.5 s were used to rule out the possibility that bees might take variance into account only if the means were equal but not if one alternative was more rewarding (higher mean) than the other. To encourage the bees to switch feeders, there was no reward for 4 s after a rewarded visit. Otherwise the bees would have learned to forage exclusively on the same feeder. Each of the three phases consisted of ca. 400 visits (we always allowed the bee to finish its foraging bout). The location of the feeders was randomized between the experimental days. Each reward combination took 1 day to test. Therefore the whole experiment took 3 days for each bee.

The landing platforms of all four feeders were marked with blue tape. Thus the feeders were recognized and learned according to their location relative to each other and to landmarks further away. The reward provided by the feeders was always 35% sucrose solution (by weight). We analysed the choice behaviour by pooling the visits to the two feeders with the same reward conditions, except when revisits (visits to the same feeder) were analysed, when data for each of the four feeders were treated
separately. Since we were interested in which strategy bees adopt when they are allowed to adjust their choice behaviour to the actual reward volumes and variances, we analysed only the last 100 visits, since visual inspection of the data showed that the experimental bee had by then adjusted its choice behaviour to the reward conditions.

Data Analysis

The data files created by the PC program were checked for consistency and processed by various custom-made C and Perl programs. Inconsistent data files were disregarded. There were two sources of inconsistencies: (1) more than one bee foraging on the patch of feeders; and (2) electronic component failure. Both events were rare: less than 5% of the data files were disregarded on these grounds.

We used CSS Statistica (Statsoft) and X-SPSS Win (SPSS). Statistical methods not included in these packages were implemented in C. These were (1) regression with replication (one tailed, Zar 1984, pp. 278–283; Sokal & Rohlf 1995, pp. 476–486); (2) comparing slopes obtained from regression with replication (one tailed, Sokal & Rohlf 1995, pp. 493–499); (3) analysis of covariance, used for comparing slopes and intercepts in cases where simple linear regression was applicable (one tailed Zar 1984, pp. 300–302; Sokal & Rohlf 1995, pp. 491–521). All statistics were performed on logit-transformed proportions (Sokal & Rohlf 1995, page 761).

RESULTS

Calibration

We did calibration experiments with four bees. These bees always licked all the sucrose solution available at a particular visit. A Kolmogorov–Smirnov test for normality with a Liliefors correction showed no significant deviation from normality ($P<0.1$) for each bee and reward class. To compare the licking rates of the bees, we calculated a linear regression between licking time and weight gain. Since all data for each regression were obtained from a single bee, we could not use regression with replication, which expects independent multiple measurements for each $X$. We therefore used the mean weight gain for each bee and its lick time. The regression was significant for all bees. All correlation coefficients were significant and all slopes differed significantly from zero. None of the intercepts differed from zero. Since all regressions were significant, the slopes and intercepts of all four bees were compared with analysis of covariance. Neither slopes ($F_{3,16}=2.93$, NS) nor intercepts ($F_{3,19}=1.70$, NS) differed significantly. Therefore the data were pooled and a regression with replication calculated (Fig. 3). The regression was significant ($F_{1,17}=37.5$, $N=24$, $P<0.001$) and no deviation from linearity was observed ($F_{5,17}=0.02$, NS). Using a density of ca. 1.17 mg/µl at 22°C for 35% sucrose solution the regression yields a rate of 1.09 µl/s (65.4 µl/min). Since licking time is a direct measure of sucrose solution volume imbibed, we use licking times as a measure of the amount of reward consumed.

Figure 2. The experimental procedure. The arrow ‘Foraging bouts’ shows in which bout of foraging the bee made its choice of which feeder to visit; the arrow ‘Choices’ indicates the succession of visits to feeders during the experiment. The two boxes represent the two alternative food rewards offered: the amount of reward (available for 2.5 or 0.5 s) and the reward’s variance state, constant (C) or variable (V). After ca. 400 visits to all feeders (depending on when the foraging bout was finished) the variance state of one of the alternatives was changed (phase 2) and after another 400 visits the variance states of both alternatives were changed (phase 3). The star and plus signs indicate the visits to the rewards used for calculating the preference for the constant 0.5-s (*) and the constant 2.5-s (+) rewards. The reward values shown are an example. The same procedure was carried out for reward values 1.0 s/2.0 s and 1.5 s/1.5 s. See text for further details.
Do Bees Perceive Amounts and Variances Offered?

To test whether bees are able to perceive amounts and variances offered, we did two analyses. We calculated the proportion of visits to the feeders with the higher rewards (choice proportion) by pooling the visits to the two feeders that offered the same reward. Only experiments in which constant versus variable feeders were presented were included in the analysis. To avoid duplicating data, we randomly assigned the 1.5 s C/1.5 s V or 1.5 s V/1.5 s C case, ensuring that the 1.5 s V of the first case was not included in the second. A total of 11 bees and 86 experiments were included in the data set (Fig. 4). Choice proportions were logit transformed and a two-way ANOVA was performed (factor 1: mean reward, three levels; factor 2: variance type, two levels). A significant effect of mean reward ($F_{2,37}=10.3, P<0.001$) but not of variance ($F_{1,37}=0.04, NS$) was found.

The interaction (mean reward X variance type) was not significant ($F_{2,37}=1.3, NS$). However, owing to the large standard deviation of the 2.5-s V data the lack of interaction should be treated with care. Thus, bees chose the more rewarding feeders more often and seemed to ignore the variance. A post hoc Scheffé test showed significant differences between the mean rewards 1.5 s/2.5 s and 2.0 s/2.5 s ($P<0.01$). The bees adjusted their choice proportions to the mean rewards offered.

To see whether the amount of each single reward was perceived, we analysed the immediate revisit behaviour to the just-rewarded feeder (stay flights; see Greggers & Menzel 1993). The licking times at variable feeders (range 0.01–10.38 s; $N=1114$) were split into bins of approximately equal size. We could not use equal-sized bins for the following reasons. Assume a required bin size $K=100$ and an almost full bin (1.10 s, 0.19 s) with $K=90$ observations. Owing to the limited accuracy in measuring the licking times (10 ms) and the large $N$, we have 20 observations of 0.20 s. We cannot extend and add to the existing bin ([0.10 s, 0.20 s] would yield $K=110$) nor can we close it and start a new bin ([0.10 s, 0.19 s] would yield $K=90$). The only way to achieve $K=100$ would be to split the 0.20-s observations between two bins, which, in our opinion, is worse than using slightly different bin sizes. The number of visits included in these bins ranged from 84 to 126. For each bin the proportion of immediate visits following the rewarded visit was calculated and plotted against the mean reward of the visits included in this bin (Fig. 5). The proportions of immediate revisits were logit transformed and a regression analysis was performed on these data as depending on the lick time. The linear regression was significant ($r=0.89, F_{1,77}=283, N=79, P<0.001$). The slope was significantly different from zero ($b=0.35, t_{77}=16.8, P<0.001$). Therefore, the probability of an immediate revisit increased significantly with the amount of reward encountered on the previous visit. The data in Fig. 5 include both rewarded and unrewarded immediate revisits. Since zero rewards may influence risk sensitivity (Shafir et al. 1999), we calculated the
percentage of zero rewards depending on reward volume and variance state (Table 1). The frequency of zero rewards increased with increasing reward (as in Fig. 5) and did not differ between the constant and variable feeders.

**The Influence of Reward Variance**

To analyse the influence of variance on choice behaviour, we did 40 experiments in 24 days, with nine bees making 15,867 choices. We used the following method to distinguish the influence of reward combination and variance on choice behaviour. The choice proportions during phase 1 of the experiment (in which both rewards were offered in a constant state) were taken as the reference for the respective reward in the following phases of the experiment. From these proportions we subtracted the choice proportion observed in the phase of the experiment where this reward was offered in variable states. Consider the following example. In the first phase of the experiment we offered 0.5 s C/2.5 s C (A); in the second phase 0.5 s V/2.5 s C (B); and in the third phase 0.5 s C/2.5 s V (C). Results from A provided the reference for both 0.5 s and 2.5 s. Subtracting the choice proportions for 0.5 s at B from that at A gives the preference for the constant feeders for 0.5 s, and subtracting the choice proportion for 2.5 s at C from that of A yields the same value for 2.5 s (see also Fig. 2). This method leads to two data points per bee and day. Negative differences would indicate preference for the variable feeders and, therefore, risk proneness; positive differences would indicate preference for the constant feeders and, therefore, risk-averse behaviour.

As Fig. 6a shows, 85% of the differences (34 of 40 observations) fell in the interval [-10%, 10%]; three of the six differences observed outside this interval were obtained from a single bee. There were 25 observations of negative differences and 15 of positive differences. The slightly higher frequency of negative differences might indicate a tendency to risk proneness. These data consist of a mix of dependent (multiple measurements per bee) and independent (from multiple bees) data. For statistical analysis we calculated for each bee a mean risk preference (Fig. 6b) and performed a one-tailed t test testing the $H_0$ that the mean risk preference for all bees is 0%. This yielded a $t_n=0.93$, $N=9$, NS. Four bees were risk averse (1.9, 2.8, 1.2 and 1.5%) and five bees were risk prone (-4.6, -1.3, -7.3, -1.5 and -7.0%). However, deviations from risk indifference were only marginal (Fig. 6b). Since unrewarded immediate revisits occurred, an additional source of variance was introduced by the bees’ choice behaviour itself. Thus constant feeders were not really constant but low-variance feeders, and variable feeders had a higher variance. To test for any influence of the amount of variance, we calculated in the same manner as for the choice proportions the differences between

![Table 1. The percentage of zero rewards encountered for all reward volumes (lick times) and variance state combinations used](image-url)

<table>
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<tr>
<th>Lick time (s)</th>
<th>Constant</th>
<th>Variable</th>
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<td>7</td>
</tr>
<tr>
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<td>13</td>
<td>16</td>
</tr>
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<td>2.5</td>
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![Figure 6. (a) Preference of bees for feeders differing in reward variance. Negative values indicate a preference for the variable reward; positive values indicate a preference for the constant reward. See Results for calculation of preference values. (b) For each individual bee the mean SE (□) and SD (vertical bars) of the data presented in (a) are shown. Statistics are based on these data. (c) Relative preference values (as in a) plotted as a function of difference in reward variance between constant and variable feeders. Note that the constant feeder also had an effective reward variance, although small, because of unrewarded immediate revisits (see text).](image-url)
the standard deviations for constant and variable feeders. The amount of difference in variance did not affect the result (Fig. 6c), giving further indication that bees behaved indifferently to reward variance.

DISCUSSION

Bees distributed their choices with respect to the amount of reward, and they perceived differences in the amount of reward as experienced in the sequential visits at the variable feeders. Thus the bees perceived the amount and variance of the sucrose solution offered. Their choice behaviour was consistent with a risk-indifferent strategy. These results were obtained with an automated set-up in which normally distributed rewards could be offered and which allowed us to exclude various sources of potential experimental errors (see Introduction). Moreover, in contrast to the majority of other studies of risk sensitivity in bees, we also considered and analysed the variance introduced by the bees’ choice behaviour itself, induced by their immediate revisits to just-depleted feeders. The results are bound to the design of our experiment, and generalization is difficult. Our test bees experienced constant feeders first, and were then shifted to a choice between constant and variable feeders. We cannot rule out that their choice behaviour was influenced by the initial training phase to constant feeders, but we believe that this effect is negligible for the following reasons. (1) Bees learned the arrangement of feeders very quickly and adjusted to different reward rates within a few bouts. (2) Changing the position of feeders led to a quick adjustment of choices. (3) Bees made 300 visits during ca. eight bouts before we used the data for analysis of choice properties. At that time, bees had most likely fully adjusted to the new conditions. (4) The observed undermatching indicates oversampling and should facilitate a quick response to changing conditions. It thus appears that the amount of pretraining to constant feeders did not affect choice proportions after training sessions of various durations.

Calibration

There was a strong linear relationship between licking time and the weight gained by the bees. This was true for each individual bee and for the pooled data. Since weight gain is a direct measure of the volume of sucrose solution imbibed by the bee, our method allowed us to control the amount of sucrose solution offered by the feeders. Since we let the bee gain approximately the same weight at each reward time, this resulted in more measurements at shorter licking times and thus in increasing variance with increasing licking time. Thus in Fig. 3 mean and variance are correlated, which, strictly speaking, violates an assumption of linear regression. We performed the same analysis for the weight gain rates, where the variance was homogeneous. Results of both analyses differed only marginally (0.93 mg/s versus 0.91 mg/s). Núñez (1966) reported licking rates of 100 μl/min for 21% (by weight) sucrose solution and 82 μl/min for 42% (by weight) sucrose solution. Our observed licking rates (53.42–76.87 μl/min for 35% (by weight) sucrose solution) are consistent with these values.

Bees Perceive the Amounts and the Variances Offered

Bees distributed their choices among all feeders, that is, they visited each of the four feeders. Greggers & Menzel (1993), who also used four feeders but with different flow rates of sucrose solution, showed that for flow rates lower than 1 μl/min, bees match their choice proportions to the respective flow rates offered by four different feeders providing four different flow rates. They further found that bees use the location of the feeders to identify them (see also Greggers & Mauelshagen 1997). Our results corroborate these findings and prove that bees distributed their choices according to the amount of mean reward offered. As in Greggers & Menzel’s (1993) study, bees tended to undermatch higher reward rates, a phenomenon explained by the assumption that bees also learn the whole patch of feeders and thus transfer choices to the feeders with low reward rates. This indicates that bees were able to discriminate the feeders using their position relative to landmarks, and to relate their respective reward rates to them. The accelerating relationship between mean reward offered and choice proportion did not differ between constant and variable feeders, meaning that the bees were able to assess at least an estimate of the mean reward in the variable feeders. The significant accelerating relationship found between the amount of reward and the proportion of immediate revisits further supports this assumption, because it shows that bees were able to perceive the amount of each single reward they obtained, as they modulated the intensity of their revisit behaviour linearly according to the amount of reward obtained last. It is unlikely that this behaviour is due to the use of a scent mark (Giurfa & Núñez 1992), the intensity of which would have to indicate the amount of reward received, because control experiments by Greggers & Menzel (1993) ruled out this possibility for a similar set-up and similar choice frequencies. Rather, we believe it indicates a response to an observed difference between the expected and the obtained reward. Therefore the bees had access to both parameters needed for calculating the variance: the mean reward and the amount of reward obtained at each single visit. Although this does not directly show that they can perceive variance (the only way to show this would be to show an influence of variance on behaviour), it is likely that the bees use the parameters to which they have access, and we conclude that in our study the bees were able to perceive both the amount of, and the variance in, sucrose solution offered, but were nevertheless risk indifferent.

The Influence of Reward Variance

Reward variance had no significant effect on choice behaviour. There was a slight but nonsignificant tendency to risk-prone behaviour. If Greggers & Menzel’s...
(1993) model were to apply to our experiments, we would expect risk proneness, because of the stronger excitatory learning during positive deviations from the expected amount of reward than during inhibitory learning when negative deviations are experienced. This should facilitate choosing the variable feeders. The effect was much smaller in our experiments than in Greggers & Menzel's (1993) study, because the differences in the amount of reward were larger in the latter. This is due to bees in Greggers & Menzel’s (1993) study experiencing volume differences between zero and a multiple of the ratio between lowest and highest flow rate (1:8), because not visiting the feeder with the highest flow rate for a while led to a larger accumulated volume than the ratio of the flow rates.

The environmental conditions experienced by the bees should, according to optimal foraging theory, result in risk-averse behaviour. Thus this theory is not supported by our data. However, bees are able to recognize differences in the amount of reward well below the standard deviations used to generate variance. Therefore, bees might be insensitive to variance, not because they cannot detect and learn the small differences in the amount of rewards, but rather because they appear to eliminate the parameter reward variance when they choose a particular feeder and refer only to the mean amount of reward rate of that feeder. There are two possible explanations: (1) bees may have a short-term working memory unable to keep track of the change in reward quantity over time, or, from another perspective, may have a small working memory allowing them to store only a few reward experiences; or (2) they are able to monitor the changes in reward quantities over time and over a string of events, but they eliminate this parameter and behave only according to the mean of reward quantity. The first possibility can be ruled out. Greggers & Menzel’s (1993) findings with respect to the asymmetry between positive and negative deviations from the expected amount of reward can be explained only if bees store the experiences of quantities of rewards during at least several successive visits (Menzel 1999).

We believe that our reward conditions represent the natural situation in the flower market. If this is true, lack of sensitivity to variance is not a failure of performance, or a limitation of memory processing, but rather an adaptation to cope with the unreliability of scattered food sources such as flowers. Flowers may also be exploited by other foraging animals and thus variance in amount of reward is a weak measure of their productivity which is dependent upon environmental factors and the flower’s functional status. Such a complex constellation of multifaceted parameters might better be reduced to a single important parameter, average profitability. The strategy leading to such parameter contraction could result from two counteracting processes: risk proneness as a consequence of learning rules and risk aversion as an adaptation for coping with the law of diminishing returns. Such an argument assumes a cost of neural processing of complex parameter constellations. We might argue that the limited capacity of working memory in bees might be related to this cost, because if too much of the working memory is allocated to tracking reward variance too little might be left for other important parameters (such as spatial arrangement of flowers, the sensory cues and their handling requirements).

The question of risk sensitivity in foraging hymenoptera is a controversial issue. Experimental evidence has been presented both in favour of risk sensitivity (Real 1981; Waddington et al. 1981; Real et al. 1982; Harder & Real 1987) and against it (Waddington et al. 1981; Waddington & Gottlieb 1990). The balance between the two processes suggested above may be very sensitive to the particular experimental conditions. For example, it may be important whether the animal experiences zero reward when extending the proboscis, a situation that probably never exists under natural conditions, or whether probing for a reward with the proboscis leads to stimulation with pure water. Shafir et al. (1999) tackled the first question and concluded that bees may be sensitive to zero rewards. In our experiments both constant and variable feeders offered a similar percentage of zero rewards. Our findings could be explained if bees were to take zero rewards into account while evaluating variability (Shafir et al. 1999), but (1) it is unlikely that bees rely only on zero rewards, which are uncommon in a natural context, and (2) the variance created by the zero rewards was low compared with the induced variance. Thus zero rewards alone should not lead to risk indifference. Several studies have used pure water as a stimulus, but it is particularly problematic, because water at a food site has an aversive component, but the strength of aversiveness depends on weather and colony conditions. Our experimental conditions were designed according to these arguments and appeared to resemble natural conditions more closely. We thus conclude that, under natural conditions, choice behaviour of bees is not guided by risk sensitivity.

Acknowledgments

Uwe Greggers contributed considerably to the design of the feeders. We thank Dr M. Giurfa, Dr L. Chittka and two anonymous referees for valuable comments on the manuscript. This study was supported by the Berlin-Brandenburgische Akademie der Wissenschaften (stipend to A.F.) and the Deutsche Forschungsgemeinschaft (grant no. Me 365/20-2 to R.M.).

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