Automata, Matching and Foraging Behavior of Bees

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Using the approach of bounded rationality and myopic learning, we attempt to explain why bees (as examples of a forager animal) do the right (optimal) thing in an environment of many foragers, namely to adopt the Ideal Free Distribution, but do the wrong thing when they are alone, namely stick to the Matching Law. We discuss two types of simple foraging strategies for bees. Each of these explicit strategies explains that in a multi-bee community the bees will distribute themselves over the nectar sources according to the Ideal Free Distribution. At the same time, these strategies explain that in single-bee experimental settings a bee will match, by its number of visits, the nectar supply from the available sources (the Matching Law). Moreover, both strategies explain that in certain situations the bees may behave as if they are risk averse. These results indicate that a competitive market in a multi-bee community permits individuals to be boundedly rational and still forage optimally.

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1. Introduction

In animal behavior studies, many experiments of the following type have been performed (Commons *et al.*, 1982; Maynard-Smith, 1982; Staddon, 1983; Houston, 1983; Davison & McCarthy, 1988; Menzel & Gregger, 1992):

An animal subject can repeatedly choose from two different food sources that give precisely the same quantity of the same food, however with different frequencies. Suppose that, at each point in time, the yellow source Y gives one unit of food with probability p, and the blue source B gives one unit of food with probability q (and 0 units otherwise). These experiments reveal that the animal subject behaves as if, asymptotically, it matches the reward probabilities by the frequencies of visiting the alternatives, i.e. the number of visits to Y relates to the number of visits to B as p to q. This kind of behavior has been called the "Matching Law" (see Staddon, 1983; Maynard-Smith, 1984; Davison & McCarthy, 1988; Menzel & Gregger, 1992, for a detailed review on experiments, and see

Houston, 1983; Houston & McNamara, 1986; Houston & Sumida, 1987; and Krebs & Kacelnik, 1991, for theoretical considerations).

These single-animal experiments are closely related to so-called two-armed bandit problems in statistical decision theory, where a player wishes to maximize his profits from playing a two-armed gambling machine of which one arm gives a greater probability of winning. The rational player, not knowing the winning probabilities of the arms, should try to find the more profitable arm and play it exclusively (DeGroot, 1970; Rotschild, 1974). A behavior of matching the success probabilities seems to be irrational (Houston *et al.*, 1982; Staddon, 1983; Real, 1992). One of our goals is to explain this "irrational" behavior by presenting simple foraging strategies that are optimal and rational in a multi-animal natural environment.

We show that in a multi-animal setting these strategies lead to what is known as the Ideal Free Distribution (IFD: Fretwell, 1972; Milinski & Parker, 1991). Peleg & Shmida (1992) have proved the

existence of the IFD in a general framework of an environment with many types of flower and bee. To explain briefly the IFD, consider n (identical) animals and two food sources Y and B where food is being supplied with rates p and q respectively. Then after some time a fraction $p/(p+q)$ of the animals will be feeding at the Y source while a fraction of $q/(p+q)$ will be at B. Thus, the number of animals at Y relates to the number of animals at B as p to q. In a natural multi-animal situation, establishing the IFD seems to be the rational thing to do, since at the IFD the average intake of food is the same at all food sources, so no animal can improve its payoff by feeding at another food source: game-theoretically we have a Nash equilibrium. When non-cooperatively trying to establish the IFD is the "natural" thing to do for the animal, then in an artificial single-animal setting one may observe irrational behavior.

When applying our strategies to a situation where the animal can choose between two probabilistic food sources in which the food supply is normally distributed with the same mean but with different variances, our result shows that the animal may act as if it is risk-sensitive (*sensu* Real & Caraco, 1986). An animal will act as if it is risk-averse if its (individual) critical level is smaller than the mean, and risk-prone otherwise. Here the critical level is a threshold by which the animal judges each quantity of food it obtains as being satisfactory or not. The animal will prefer the food source with the smallest probability of getting something below critical level.

For simplicity, we shall focus on bees foraging for nectar instead of general animals in this paper, but very similar ideas apply to a wide variety of choices animals make between alternative reward sources and for different types of rewards (food, mates, territory, etc.). Most of the wild bees, especially in the Mediterranean area, are solitary and live for about four to five weeks (Shmida *et al*., 1993). Each female has its own nest and raises its brood alone. There is no exchange of foraging information among bees. Each bee is assumed to be a maximizer of Darwinian fitness (Hammerstein & Selten, 1993), i.e. it maximizes its average nectar intake per time unit. Nectar will be considered as the only reward for the bee in the model. Nectar is produced by flowers for the sole purpose of attracting pollinators. Bees have no innate preference to particular flowers (Heinrich, 1979; Menzel, 1985, 1990; Menzel & Shmida, 1992) and their foraging patterns appear to be influenced by experience. Our approach is based on the assumption, derived from recent experimental studies, that bees use mainly their short-term memory for decision-making in local flower patches (Menzel & Gregger, 1992) and use simple decision rules, taking into account only the last one or two flowers, in the process of deciding on leaving or staying in a patch of a given flower type (Real *et al*., 1990; Cresswell, 1990; Real 1991, 1992; Kadmon & Shmida, 1992; Kadmon *et al*., 1992). These experimental results suggest that the bees have bounded recall. The strategies we provide are described by finite automata (Ben-Porath & Peleg, 1987; Kalai, 1990) by which the bees respond only to their own payoffs and remember only payoffs of the last few visits. In this paper we do not include travel or handling times for the flower types. These parameters are considered in some other models (Laverty, 1980; Harder, 1987; Friedman & Shmida, 1992; Peleg & Shmida, 1992).

The two explicit strategies examined in this paper are the *ε-sampling strategy* and the *failures strategy*. Briefly, one could say that the ϵ-sampling strategy is to visit one alternative repeatedly, but every now and then sample the other alternative and switch if the other alternative is better than the one previously selected. The failures strategy describes an innate behavior leading to matching according to some simple finite automaton (e.g. leave Y after y empty flowers, leave B after b empty flowers). The two behavioral strategies represent two alternative approaches to model choice rules of foraging animals: resource dependent moves vs. resource independent moves. These strategies will be discussed in Sections 2 and 3 respectively, each with respect to multi-animal and single-animal settings and in relation to risk. Section 4 concludes with some discussion on related literature.

To simplify notations we restrict our attention to the situation where there are only two food sources: Y (yellow) and B (blue). However, our results can be extended to situations with any finite number of food sources.

2. The ϵ-Sampling Strategy

The ϵ-sampling strategy is briefly described as follows. A foraging bee which has to choose between two colored resources will use the following rule: initially choose one of the colors at random, then at each point in time stay at the current color with probability $1-\epsilon$ and sample the other color with probability ϵ; when sampling, if you find a payoff above your critical level, then switch to this new color, otherwise return to the previous color immediately; at this next color (new or old) again at each point in time stay with probability $1-\epsilon$, sample elsewhere with probability ϵ. This ϵ-sampling strategy is close to Heinrich's (1979) idea of "Major–Minor behavior" of bees, which motivated our research. We formally define the ϵ-sampling strategy and the critical level

below. The bee's critical level is a dynamic function of its memory where most recent experiences are reflected strongest. For the reflection of memory we use a parameter $\alpha \in (0, 1)$.

DEFINITION 2.1. *Let* α, $\epsilon \in (0, 1)$, *let* $a(t) \in \{Y, B\}$ *represent the action selected and let* $r(t) \in \mathbb{R}$ *be the payoff at time* $t \in \{1, 2, 3, \ldots\}$. *Define* $cl(1) = 0$ *and*

$$cl(t+1) = \alpha cl(t) + (1-\alpha)r(t) \qquad (1)$$

for $t \geqslant 1$. *Then* $cl(t)$ *is called the critical level at time* t. *Let* Y_ϵ *denote the mixed action: choose* Y *with probability* $1-\epsilon$ *and* B *otherwise and let* B_ϵ *be defined similarly. The ϵ-sampling strategy is defined by playing:*

at $t = 1$ *use* $Y_{0.5}$,
at $t = 2$ *use* $a(1)_\epsilon$,
at $t > 2$ *use* $a(t-1)_\epsilon$ *in case* $a(t-1) \neq a(t-2)$ *and* $r(t-1) > cl(t-1)$, *use* $a(t-2)_\epsilon$ *otherwise.*

Note that eqn (1) is the linear operator function originally used by Bush & Mosteller (1955). In this definition the parameters α and ϵ are the individual bee's factors. The first one is related to memory and the second one to searching elsewhere. Those familiar with game theory can think of ϵ as a bee's *trembling hand* (Selten, 1975) trying to play a pure action. We wish to emphasize that different individuals may have different parameters, but our results remain the same.

Consider what happens if we have a population of $n \in \{1, 2, 3, \ldots\}$ bees that are foraging on two patches of flowers, a yellow patch Y and a blue patch B. Per unit of time, the yellow patch has a total nectar supply of $y > 0$, while there is a total quantity $b > 0$ at patch B. We make the following assumptions:

(i) The total quantity of nectar at Y is equally distributed over the visiting bees at Y at each stage; that is, if at some stage $t \in \mathbb{N}$ there are n_Y bees at Y, then we assume that at this stage each of these bees is receiving $r(t) = y/n_Y$ units of nectar. Likewise for B.

(ii) There is no accumulation of nectar at a patch. All nectar is taken by the bees at each stage and if at some stage there are no bees at a patch then at the next stage the total quantity is still the same.

(iii) The bees' sampling factors ϵ are sufficiently close to 0 to have a negligible probability of two or more bees moving at the same time. Thus the distribution of bees over flower types changes by one bee moving either from Y to B or from B to Y. (Here "moving from Y to B" means: previously the bee was at Y, now it has gone to B for a sample and since the payoff received at

B is larger than the critical level it decides to stay at B.)

(iv) We assume that, when going out sampling, the bee has been in Y sufficiently long to have its critical level close to y/n_Y.

THEOREM 2.2. *Under the above assumptions the population will stabilize in the Ideal Free Distribution.*

Proof. First, observe that, due to its ϵ, each bee will go out sampling the other color infinitely often. Hence, if the process stabilizes in some distribution of bees over Y and B, then it must be such that no single bee can strictly improve its payoff by moving to the other color. Second, observe that whenever a bee moves from Y to B we must have that $y/n_Y < b/(n_B + 1)$, where n_Y and n_B are the numbers of bees before the move at Y and B respectively.

We now define a *potential function* (Monderer & Shapley, 1988) on the distributions of bees as

$$P(n_Y, n_B) = y \sum_{m=1}^{n_Y} 1/m + b \sum_{m=1}^{n_B} 1/m, \qquad (2)$$

where $\Sigma_{m=1}^{0} 1/m$ is understood to be equal to 0. If a bee moves from Y to B, then the distribution changes from (n_Y, n_B) to $(n_Y - 1, n_B + 1)$. At the same time the potential changes from $P(n_Y, n_B)$ to $P(n_Y - 1, n_B + 1)$. Now $P(n_Y - 1, n_B + 1) - P(n_Y, n_B) = b/(n_B + 1) - y/n_Y > 0$, because the bee decided to stay at B. Hence, with each bee movement the potential strictly iicreases. Since there are only finitely many distributions of the n bees and since the bees will keep moving as long as possible, the potential function will eventually reach its maximum. At this maximum we have that $y/n_Y \geqslant b/(n_B + 1)$ and $b/n_B \geqslant y/(n_Y + 1)$; hence

$$y/n_Y \approx b/n_B \qquad (3)$$

and the population has reached the IFD. □

We remark that a stable situation that arises from all bees doing ϵ-sampling strategies, needs not be Pareto-optimal, i.e. there may exist an alternative distribution for which all bees have a higher payoff. Take, for example, four bees, 8 units of nectar at Y and 1 unit of nectar at B. For this situation the IFD will be that all four bees will go to Y and the 1 unit at B is not being consumed. Thus each bee obtains a payoff of 2 all the time. The bees could all improve their payoffs by visiting B in turns, giving each bee the average payoff $9/4 > 2$. In the case of infinitely many bees, the distribution obtained from the ϵ-sampling strategies will indeed be Pareto-optimal, so that in a natural

environment with many bees and flowers the IFD solution obtained is practically Pareto-optimal.

Let us now see what happens if we take a single bee for an experiment of the following type (Fig. 1). We have two artificial (Bernoulli) flowers Y (yellow) and B (blue). Each time the bee visits the yellow flower it will receive 1 unit of nectar with probability p and 0 units otherwise. Equivalently, in a natural situation one can think of a patch of yellow flowers, where a p-fraction of the flowers is full, while a $(1-p)$-fraction is empty. For the blue flower we have probability q for a full flower. As before, let ϵ be the bee's sampling factor. Using the ϵ-sampling strategy, the bee will always have a critical level in between 0 and 1, and it will decide to stay in the sample color if and only if it finds a full sample. If the bee applies the ϵ-sampling strategy, then its behavior corresponds with the Markov chain depicted in Fig. 1. In this figure Y_1 and B_1 correspond to the sampling stages at the respective colors; one gets there by sampling probability ϵ and one decides to remain (or else to return) with probability p and q respectively. Consequently, Y_2 and B_2 represent situations where the bee has decided to stay in the particular color.

Computing the stationary distribution of this Markov chain, one finds that the number of visits to Y relates to the number of visits to B as $p+q\epsilon$ to $q+p\epsilon$, which is approximately as p to q if ϵ is small. Thus we have the following theorem.

THEOREM 2.3. *If ϵ is small, then a bee applying the ϵ-sampling strategy in a single-bee experiment will exhibit matching the payoff probabilities by the frequency of its visits* (*the Matching Law*).

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Consider a single bee foraging on two patches Y and B, in which all flowers have a normally distributed nectar supply with a common mean μ, but where the distributions differ in variance; for the yellow flowers the variance is v_Y while for the blue ones it is v_B.
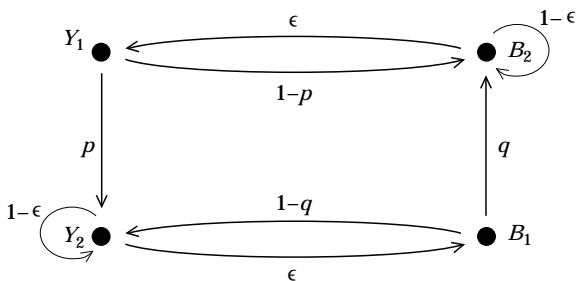

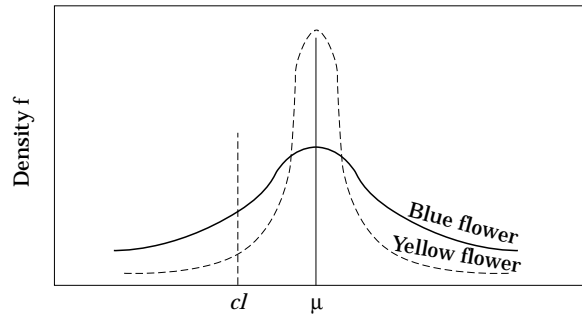
FIG. 1. Markov chain for the ϵ-sampling strategy.

FIG. 2. Two patches of flowers with normal nectar distributions.

THEOREM 2.4. *Suppose that the bee is using the ϵ-sampling strategy and has a fixed critical level cl to decide whether any flower is full or empty. Without loss of generality we assume $v_Y < v_B$. If $cl < \mu$, then the bee will act as if it is risk-averse, i.e. it will spend more time on Y than on B. If $cl > \mu$, then the bee will act as if it is risk-prone, i.e. it will spend more time on B than on Y.*

Proof. If $cl < \mu$, then the probability of getting a reward above the critical level is larger for Y than it is for B (cf. Fig. 2). So, when sampling, the bee will decide to move to Y more often than it will decide to move to B. Hence the result. The second part is similar. □

We are aware of the fact that assuming a fixed critical level is not very realistic, but, nevertheless, we feel that this is an interesting observation. Also, a similar assumption is quite realistic for the failures strategy, where, for a similar result, one only needs the critical level to be below, or above, the mean during the observed foraging period (cf. Section 3). It is also important to notice that the result of this theorem holds for any continuous nectar supply distributions F_Y, F_B on the interval $[\alpha, \beta]$ which have a common mean $\mu = (\alpha + \beta)/2$ and continuous derivatives f_Y, f_B for which

(i) f_i is symmetric with respect to the mean μ, i.e. $f_i(\mu + x) = f_i(\mu - x)$ for all $x \in [0, \beta - \mu]$ and $i = Y, B$, and

(ii) there is $x^* \in [0, \beta - \mu]$ with

$$f_Y(x) > f_B(x) \quad \text{if } |x - \mu| < x^*,$$

$$f_Y(x) < f_B(x) \quad \text{if } |x - \mu| > x^*.$$

It should be noted that the result depends on how $F_Y(cl)$ and $F_B(cl)$ are compared. If $F_Y(cl) < F_B(cl)$, then an ϵ-sampling bee with critical level cl will favour the yellow patch, since $F_i(cl)$ is the probability of having an empty flower at $i = Y, B$. Thus, if F_Y, F_B are nectar supply distribution functions on $(0, \infty)$ with $F_Y(r) < F_B(r)$ for all $r \in (0, \infty)$ (i.e. F_Y strictly dominates F_B according to the "first-order stochastic

dominance criterion''; Fishburn, 1976), then *every* bee that uses an ϵ-sampling strategy and judges flowers full or empty according to some critical level, will favour the yellow patch. This means that under these conditions, every bee would visit more yellow flowers than blue flowers or, in other words, spend more than half of its foraging time at the yellow patch.

One can also take nectar distributions as in Fig. 3 (or, e.g. negative exponential distributions), in which most flowers are empty or have very small nectar quantities. Such leptokertic distributions are very common in nature (Shreiber, 1993; Boker, 1993). In case the bee forages on two flower patches Y and B with distributions as in Fig. 3, then the bee will compare the two patches. If we assume that f_Y and f_B are continuous and cross each other only once (e.g. f_Y starts above f_B), then such a comparison also falls in the first-order stochastic dominance. If a bee forages on such flower patches and uses a critical level for switching between Y and B, then it will stay more frequently in the blue patch with the higher variance than in the yellow patch with the lower variance.

We emphasize that the results presented in this section do not really depend on ϵ. All that matters is that $\epsilon \in (0, 1)$ is sufficiently small to have a bee staying in the same patch long enough to get a good estimate of the payoff in this patch. One can even allow ϵ to be payoff dependent, getting smaller with high current payoffs and getting larger with low current payoffs. The only thing needed is that no matter at what color (patch) the bee is foraging, with probability 1 it will eventually sample at another color (e.g. this condition is satisfied if ϵ is bounded away from 0). In the multi-bee model the IFD result will still be valid if all individual bees have (sufficiently small) different ϵ's.
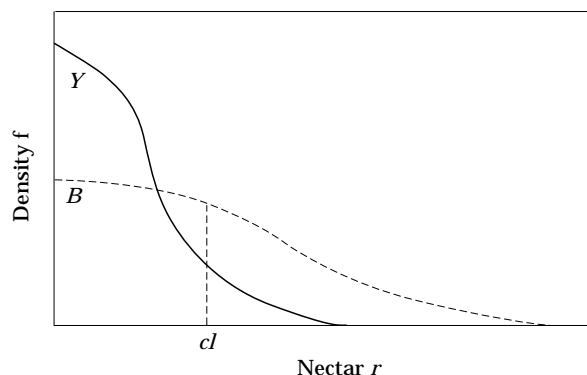

FIG. 3. Two patches of flowers with decreasing nectar distributions.

3. The Failures Strategy

In the previous section the probability of the bee going out to sample the other color was independent of the payoffs received in the current color; it was determined solely by the innate sampling factor, ϵ. In this section we present a foraging strategy which will make the bee move to another color after engaging a certain number of consecutive empty flowers. Recall that empty is to be interpreted as "below critical level". The bee is assumed to behave as a finite automaton (Neyman, 1985; Ben-Porath & Peleg, 1987; Kalai, 1990).

This automaton strategy corresponds to the well-known "area-restricted search" (Real *et al.*, 1990) of animal behavior, which was termed "near–far" by Motro & Shmida (1995). The near–far strategy is $A(1, 1)$ (see below), a special case of our automaton strategy where the bee uses only the last flower visited to evaluate the current patch. It means: stay in the patch as long as you find food and leave otherwise (similar strategies have been reviewed by Houston *et al.*, 1982). Experimental studies reveal this near–far behavior (see in Motro & Shmida, 1995).

Let us return to the experiment with two artificial flowers Y (yellow) and B (blue) that give 1 unit of nectar with probability p and q respectively (and 0 units otherwise). As already mentioned above, observations indicate that the frequencies of visits by the bee will match these probabilities. The event of receiving 1 shall be called a success, receiving 0 is a failure.

DEFINITION 3.1. *Let y, b be positive integers. The finite automaton $A(y, b)$ is given by:*

  (i) *leave Y after y consecutive failures and move to B,*
 (*ii*) *leave B after b consecutive failures and move to Y.*

As an example, we depict automaton $A(3, 2)$ in Figure 4(a), where Y_k indicates the automaton state of being at Y while the last k consecutive yellow visits were failures $(k = 0, 1, 2)$. Obviously the automaton states B_0 and B_1 are to be interpreted similarly. If the bee, in any of the automaton states, gets a full flower (1), then it goes to a new automaton state according to the 1-arrow, otherwise it goes according to the 0-arrow for having experienced a failure. The automaton corresponds with a Markov chain on the states Y_0, Y_1, Y_2, B_0, B_1, which is depicted in Figure 4(b). In this figure and elsewhere in this paper we write $\bar{p}$ to denote $1 - p$ and $\bar{q}$ for $1 - q$. This Markov chain in turn corresponds to the transition
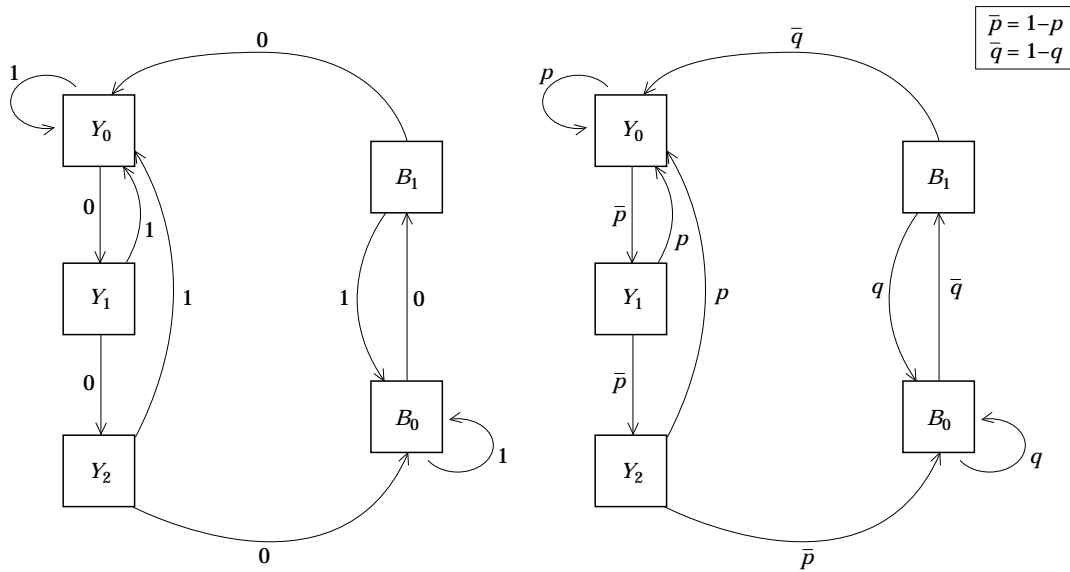
FIG. 4. (a) The automaton $A(3, 2)$ with 1-arrows and 0-arrows to indicate successes and failures, respectively. (b) The related Markov chain.

matrix T given by:

$$T = \begin{array}{c} \\ Y_0 \\ Y_1 \\ Y_2 \\ B_0 \\ B_1 \end{array} \begin{array}{ccccc} Y_0 & Y_1 & Y_2 & B_0 & B_1 \\ \begin{pmatrix} p & \bar{p} & 0 & 0 & 0 \\ p & 0 & \bar{p} & 0 & 0 \\ p & 0 & 0 & \bar{p} & 0 \\ 0 & 0 & 0 & q & \bar{q} \\ \bar{q} & 0 & 0 & q & 0 \end{pmatrix} \end{array}.$$

If the bee uses $A(3, 2)$, then we can compute its frequencies of visits to Y and B by finding the stationary distribution $\pi = (y_0, y_1, y_2, b_0, b_1)$ of T. The frequency of visits to Y is $y_0 + y_1 + y_2$ and that to B is $b_0 + b_1$. The vector π is nonnegative and adding its components gives 1. Furthermore, π has the property that $\pi T = \pi$. Using $A(3, 2)$ the bee would confirm the matching law if and only if

$$\begin{cases} y_0 + y_1 + y_2 = p/(p+q) \\ b_0 + b_1 \quad\;\; = q/(p+q) \end{cases} \tag{4}$$

The equation $\pi T = \pi$ yields

$$y_1 = \bar{p} y_0, \quad y_2 = \bar{p}^2 y_0,$$

$$b_1 = \bar{q} b_0 \quad \text{and} \quad b_0 = (\bar{p}^3/\bar{q}^2) y_0.$$

Hence we find the equations

$$y_0 + y_1 + y_2 = y_0(1 + \bar{p} + \bar{p}^2) = y_0 \frac{1 - \bar{p}^3}{p},$$

$$b_0 + b_1 = b_0(1 + \bar{q}) = b_0 \frac{1 - \bar{q}^2}{q} = y_0 \frac{\bar{p}^3(1 - \bar{q}^2)}{\bar{q}^2 q}.$$

So, if we let $f(2,3)$ denote the ratio of the frequencies

of visits to Y and B, then

$$f(2, 3) = \frac{\text{frequency of visits to } Y}{\text{frequency of visits to } B} = \frac{q\bar{q}^2(1 - \bar{p}^3)}{p\bar{p}^3(1 - \bar{q}^2)} \tag{5}$$

and the automaton $A(2, 3)$ is matching if and only if $f(2, 3) = p/q$, which is equivalent to:

$$\frac{p^2 \bar{p}^3}{1 - \bar{p}^3} = \frac{q^2 \bar{q}^2}{1 - \bar{q}^2}. \tag{6}$$

Similarly one can show the following theorem.

THEOREM 3.2. *The finite automaton $A(y, b)$ matches the payoff probabilities p and q respectively if and only if*

$$\frac{p^2 \bar{p}^y}{1 - \bar{p}^y} = \frac{q^2 \bar{q}^b}{1 - \bar{q}^b}. \tag{7}$$

We would like to remark that there are infinitely many $(y, b) \in \mathbb{R}_+^2$ for which (7) holds, because the function $y \mapsto p^2 \bar{p}^y/(1 - \bar{p}^y)$ is strictly decreasing on $(0, \infty)$ from ∞ to 0. In fact we have the following result.

THEOREM 3.3 *Let $\delta \in (0, 0.5)$ and let $M \in \mathbb{N}$ be such that $(1 - \delta)^{M-1} \leqslant 4\delta(1 - \delta^M)$. Then, for all $\delta \leqslant p \leqslant q \leqslant 1 - \delta$ there exist $y, b \in [1, M]$ with*

$$\frac{p^2 \bar{p}^y}{1 - \bar{p}^y} = \frac{q^2 \bar{q}^b}{1 - \bar{q}^b}.$$

Proof. If $p\bar{p} = q\bar{q}$, then $y = b = 1$ gives the result. Otherwise, assume without loss of generality that

$p\bar{p} < q\bar{q}$. Then

$$\frac{q^2\bar{q}^M}{1-\bar{q}^M} = \frac{q\bar{q}\bar{q}^{M-1}}{(1-\bar{q}^M)/(1-\bar{q})}$$

$$\leqslant \frac{0.25(1-\delta)^{M-1}}{(1-\delta^M)/(1-\delta)} \leqslant \delta(1-\delta) \leqslant p\bar{p}. \quad (8)$$

By continuity there exists $b \in [1, M]$ with

$$q^2\bar{q}^b/(1-\bar{q}^b) = p\bar{p} = p^2\bar{p}/(1-p). \qquad \square$$

For any p,q-situation of yellow and blue flowers with $p, q \in [\delta, 1-\delta]$ this theorem provides the existence of real numbers $y, b \in [1, M]$ for which $p^2\bar{p}^y/(1-\bar{p}^y) = q^2\bar{q}^b/(1-\bar{q}^b)$. However, to have an automaton for the bee, we need to have numbers in the range $\{1, 2,..., M\}$. We therefore propose to see (y, b) as a convex combination of pure pairs $(y^*, b^*) \in \{1, 2,..., M\}^2$ and to have the bee perform an initial randomization over the pure automata $A(y^*, b^*)$ according to the weights of the convex combination. Then, in expectation, the bee will leave Y after y consecutive failures and it will leave B after b consecutive failures. In view of the bee's bounded recall, it is worth noting that with $M=2$ one can handle δ as small as 0.22, while with $M=3$ one can handle δ as small as 0.18. Thus, for all $p, q \in [0.22, 0.78]$ one can obtain matching with automata $A(y, b)$ with $y, b \in \{1, 2\}$.

For a bee performing matching with an automaton of the above type, the number of consecutive empty flowers it allows itself to encounter in yellow can be different from that in blue. One can think of the bee as having an internal mechanism by which, after some rough estimation of p and q, the natural numbers y^* and b^* are selected. It is not necessarily true that the bee can use an automaton of type $A(x, x)$ since there does not always exist a real number $x \geqslant 1$ with $p^2\bar{p}^x/(1-\bar{p}^x) = q^2\bar{q}^x/(1-\bar{q}^x)$. If for example one takes $p=0.6$ and $q=0.8$, then such x does not exist. However, in natural situations it is frequently observed that p and q are small if there are many visits (Shreiber, 1993). Then we either have $p \leqslant q \leqslant 1-p$ or $q \leqslant p \leqslant 1-q$. The following theorem says that in this case the bees can use an automaton of type $A(x, x)$.

THEOREM 3.4. *If* $p \leqslant q \leqslant 1 - p$ *or* $q \leqslant p \leqslant 1-q$, *then there exists* $x \geqslant 1$ *such that*

$$\frac{p^2\bar{p}^x}{1-\bar{p}^x} = \frac{q^2\bar{q}^x}{1-\bar{q}^x}. \qquad (9)$$

Proof. If $p=q$ or if $\bar{p}=q$, then one can take $x=1$. Now consider $p < q < \bar{p}$. Using an automaton $A(x, x)$ the ratio of the frequencies of visits to Y and B is

(cf. example $A(3, 2)$ above)

$$f(x, x) = \frac{q\bar{q}^x(1-\bar{p}^x)}{p\bar{p}^x(1-\bar{q}^x)}. \qquad (10)$$

Then $\lim_{x\to\infty} f(x, x) = 0$ and $f(1, 1) = \bar{q}/\bar{p} > p/q$. Hence, by continuity there exists $x \geqslant 1$ with $f(x, x) = p/q$, or equivalently $p^2\bar{p}^x/(1-\bar{p}^x) = q^2\bar{q}^x/(1-\bar{q}^x)$. Obviously a similar result can be obtained for $q < p < \bar{q}$. $\square$

Suppose we have finitely many bees foraging on two patches Y and B consisting of Bernoulli flowers. At Y each flower gives 1 unit of nectar with probability p. At B each flower is full with probability q. We assume that the nectar supply probabilities are independent of the numbers of visiting bees. If in this situation each individual bee determines, by its internal mechanism, an automaton to forage on Y and B, then each of these individuals will approximately spend $p/(p+q)$ of its foraging time on Y and $q/(p+q)$ on B. Even stronger, we can say that for each individual bee the probability of being at Y at time t converges to $p/(p+q)$. Thus, by the strong law of large numbers the fraction of the number of bees we encounter at Y at time t converges to $p/(p+q)$ as t and the number of bees increase. That is, a $p/(p+q)$-part of the bee population will be at Y, while the others, a $q/(p+q)$-part, will be at B for large t and a large number of bees. In other words, one would observe the Ideal Free Distribution.

IFD WITH INFINITELY MANY BEES

Consider a population of infinitely many identical bees (think of a continuum) that are all using the failures strategy $A(r, s)$ with $r, s \in \mathbb{N}$, to forage on patches Y and B that have respectively total nectar supply y and b. The quantities are shared at each color by the present bees. Given critical levels for the bees at Y and B, the "full-flower" probabilities, p and q respectively, are determined by the proportions of bees currently present in each of the patches. This population of bees can be distributed according to the IFD, i.e. there are full-flower probabilities p and q, and related critical levels, for Y and B respectively, such that each bee using $A(r, s)$ is matching p/q, while the ratio of the fractions of bees at Y and B is y/b. More formally:

THEOREM 3.5. *If* $y > b$ *and* $ys > br$, *then there exist* $p, q \in (0, 1)$ *such that*

$$\frac{y}{b} = f(r, s) = \frac{q\bar{q}^s(1-\bar{p}^r)}{p\bar{p}^r(1-\bar{q}^s)} = \frac{p}{q}. \qquad (11)$$

Proof. For $q \in (0, b/y]$ define:

$$g(q) = \frac{(y/b)^2(1-qy/b)^r(1-(1-q)^s)}{(1-q)^s(1-(1-qy/b)^r)} \qquad (12)$$

Then g is continuous on $(0, b/y]$ with $g(b/y) = 0$ and with

$$\lim_{q \downarrow 0} g(q) = (y/b)^2 \lim_{q \downarrow 0} \frac{1 - (1-q)^s}{1 - (1 - qy/b)^r}$$

$$= (y/b)^2 \lim_{q \downarrow 0} \frac{s(1-q)^{s-1}}{(ry/b)(1 - qy/b)^{r-1}}$$

$$= \frac{(y/b)^2 s}{ry/b} = \frac{ys}{rb} > 1. \tag{13}$$

By continuity of g there exists $q^* \in (0, b/y]$ with $g(q^*) = 1$. Now q^* and $p^* = yq^*/b$ are as desired. □

Note that this theorem is a static result for the existence of the IFD with matching bees doing $A(r, s)$. The result does not provide a dynamic process of how to reach the IFD. We have to assume an infinite number of bees in order to have p and q not be affected by single bees moving from one state of the automaton to another state of the automaton. The proportions of bees in the states of the automaton have to be independent of time. With a finite number of bees the probabilities p and q would always depend on the precise number of bees in those states.

ATTITUDE TOWARDS RISK

Consider the single-bee situation of foraging on two patches Y and B, where all flowers have a normally distributed nectar supply with a common mean μ. The yellow flowers have variance v_Y, the blue ones have variance v_B.

THEOREM 3.6. *Suppose the bee is using a failures strategy and has a fixed critical level cl to decide whether any flower is full (success) or empty (failure). Without loss of generality assume $v_Y < v_B$. If $cl < \mu$, then the bee will act as if it is risk averse, i.e. it will spend more time on Y than on B. If $cl > \mu$, then the bee will act as if it is risk prone, i.e. it will spend more time on B than on Y.*

Proof. If $cl < \mu$, then the probability of getting a full flower is larger for Y than for B (Fig. 2). Hence the probability p of getting a full Y flower is larger than q for a B flower. Since the bee's mechanism will find an automaton to match p and q, the bee will spend more time in Y than in B. The second part is similar. □

It is very important to notice that the same result is valid for dynamic critical levels, by only assuming that the critical level is below, or above, the mean during the obseved foraging period. Moreover, this result can also be extended to apply to other nectar distribution functions, like the ones discussed for the ϵ-sampling strategy.

Finally, for this section, note that we have only considered finite automata of the type: leave $Y(B)$ after y (b) consecutive failures. However, one could also examine automata of a more general type. Let S, S_Y and S_B be finite non-empty sets of states with $S = S_Y \cup S_B$ and $S_Y \cap S_B = \phi$. We can describe a foraging automaton for the bee as a map $T: S \times \{0, 1\} \to S$ with the interpretation that a bee in state $s \in S_Y$ is visiting a yellow flower; if this particular yellow flower is full (empty) then the bee moves to state $T(s, 1)$ (respectively $T(s, 0)$). Further research is required to fully understand the possibilities of obtaining matching and IFD results by means of these general foraging automata.

4. Discussion and Related Literature

THE MATCHING LAW

There is much published literature devoted to the phenomena of the "Matching Law." (Some main and recent references are Simon, 1956; Herrenstein, 1970; Heyman, 1979; Commons *et al*., 1982; Houston *et al*., 1982; Houston, 1983; Staddon, 1983; Davison & McCarthy, 1988; Staddon & Horner, 1989). A reader of the above literature may be confused (as we are) by the rich and complicated details of the experimental results as well as by the theoretical analyses. There are also many versions of the mathematical formulation of the Matching Law (compare for example Krebs & Kacelnik, 1991, to Houston *et al*., 1982, to Houston & Sumida, 1987, to Davison & McCarthy, 1988, to the commentary by Herrenstein & Vaughan in Maynard Smith, 1984).

In this study we have focused on one main issue related to the matching law: why does the animal in an artificial binary choice setting behave "irrationally" and does not go exclusively to the resource with the higher probability? Instead, the matching law reveals (Krebs & Kacelnik, 1991) that the animal allocates its long-term behavior to two alternatives in proportion to the reward it obtains from them. To answer this question, we have presented boundedly rational strategies for which the irrational matching behavior is compatible with the equilibrium conditions for the natural IFD.

We have presented foraging rules that lead the forager to match over time the reward probabilities by the fractions of the visits to the alternatives. However, one should not confuse this matching law with "probability matching" (Maynard Smith, 1984). Probability matching is a foraging rule where, at each point in time, the forager is choosing an alternative

according to the observed full flower probabilities at the respective patches. While probability matching is a moment-to-moment foraging rule, the matching law describes the average behavior of the forager over an asymptotically long period of time.

LEARNING RULES

As Maynard Smith (1984) points out, a learning rule (i.e. a foraging strategy) observed in animals should have several properties:

(i) It should have the *relative payoff sum* (RPS) property, which says that, after a sufficiently long period of time, the probability of performing a certain act should equal the total payoff received so far for performing this act, divided by the total payoff received so far for all acts.

(ii) None of the available acts should ever fall to zero probability, since the environment might change.

(iii) Any naive animal should start with some prior probabilities of performing the different acts.

(iv) Recent payoffs should have a bigger effect on behavior than early ones (discount factor).

A strategy having these properties is Harley's RPS rule (Harley, 1981; Maynard Smith, 1984). For a two-choices situation (Y, B) this rule is defined as follows (Harley, 1981):

Let $r_Y, r_B > 0$ (residual values) and let $0 < x < 1$ (memory factor). Let $P_i(t)$ denote the payoff in $i \in \{Y, B\}$ at time $t \in \mathbb{N}$. Now let $S_i(0) = r_i$ and for $t \geq 1$ define

$$S_i(t) = xS_i(t-1) + (1-x)r_i + P_i(t). \qquad (14)$$

At time t choose alternative $i \in \{Y, B\}$ with probability

$$f_i(t) = \frac{S_i(t-1)}{S_Y(t-1) + S_B(t-1)} \qquad (15)$$

"In words, the (this) RPS rule says the following: display most frequently the behaviour which has, up to the present, paid the most, but only in proportion, roughly, to its cumulative payoff relative to the overall total" (Harley, 1981).

Although this rule is fairly simple, the foraging animal is required to adjust its probabilities of choosing either Y or B at each point in time. In contrast we have presented an explicit "molecular" ("moment to moment" in Krebs' and Kacelnik's terms) strategy that has the above properties, but for which the foraging animal will only switch every once in a while. Notice that Harley's rule assumes the animal to update probabilities at all time points and chooses Y or B independent of the patch it is currently visiting. We

question whether bees are capable of updating and computing probabilities before each visit (10 to 40 visits per minute!). Our foraging strategies give the same results while the bee is following very simple movement rules. For the sampling strategy, the way of updating the critical level should not necessarily be as in eqn (1). In fact, we only use the fact that the critical level at any stage depends on the critical level at the previous stage and on the previous payoff, while if the same payoff is given repeatedly, then the critical level converges to this payoff.

DIFFERENT CONSUMPTION POTENTIALS

We can use ϵ-sampling also in this case to reach the IFD, as can be seen from an alternative potential function (Monderer & Shapley, 1988). Thus, the potential function approach gives us a simple, quite general, but explicit, dynamic mechanism of how foraging animals can reach the IFD.

Consider a population of ϵ-sampling bees with different consumption potentials (CP). Different body sizes of bees are an example of different consumption potentials. However, the relation between size and CP does not need to be linear, but only positive monotonic. We show that a population of ϵ-sampling bees with different CPs will stabilize in the IFD, that is, $y/n_Y \approx b/n_B$ where n_Y and n_B are the total CP at Y and B respectively. To see this we define the alternative potential function P'.

$$P'(n_Y, n_B) = \min\{y/n_Y, b/n_B\} \qquad (16)$$

for $n_Y \neq 0$ and $n_B \neq 0$, while $P'(0, n_B) = b/n_B$ and $P'(n_Y, 0) = y/n_Y$.

If we have a finite number of bees with CPs in $[1, k]$, where k is the maximum CP present, then the population has the IFD if and only if $y/n_Y \geq b/(n_B + i)$ and $b/n_B \geq y/(n_Y + j)$, where i (j) is the smallest CP present at Y (respectively B). Notice that, if $n_Y \neq 0$ and $y/n_Y < b/(n_B + i)$, then $y/(n_Y + j) < y/n_Y < b/(n_B + i) < b/n_B$ implying that no bee will move from B to Y. On the other hand, a bee with CP i sampling from Y to B would decide to stay at B. There is at least one bee with CP i at Y and hence, by the ϵ-sampling strategy, at least one bee will move from Y to B. Suppose that it has CP $x \geq i$. Then the distribution changes from (n_Y, n_B) to $(n_Y - x, n_B + x)$ and $P'(n_Y - x, n_B + x) = \min\{y/(n_Y - x), b/(n_B + x)\} > y/n_Y = \min\{y/n_Y, b/n_B\} = P'(y/n_Y, b/n_B)$. Hence, with each moving bee P' is strictly increasing and the process will reach a (local) maximum after a finite number of moves. At this (local) maximum the population is in an IFD. Note that, if all bees have the same CP (as we have in Section 2), then every local maximum of this alternative potential function P', as

of the original potential function P, is necessarily a global maximum.

MILINSKI FISHES

Our ϵ-sampling strategy explains explicitly the dynamics in which "Milinski fishes" reach the IFD (Milinski, 1979, 1984; Godin & Keenleside, 1984; Milinski & Parker, 1991). Each fish has to remember only an estimate of the average payoff received so far in the old resource, and to compare it with the current payoff in the new food source when sampling. If the current payoff is higher, the fish stays; if it is lower, it goes back to the old food source. This biological behavior corresponds to the potential function of Monderer & Shapley (1988). Milinski & Parker (1991: 144) have a stationary model of the IFD with foraging fishes, but they do not have an explicit dynamic model by which the fishes can reach the IFD. Their model (including Parker & Sutherland, 1986) can be viewed as a special case of the short-run stable matching of Peleg & Shmida (1992) where the fishes' different competitive weights correspond to the bees' different handling times (technological abilities, *sensu* Selten, 1978).

Godin & Keenleside (1984) have shown experimentally that the IFD can be achieved through "sampling." However, no explicit strategy has been suggested in the literature of how fish carried out the sampling procedure. Our ϵ-sampling strategy corresponds to the "Major–Minor behavior" of bees, which has been observed in bumblebees by Heinrich (1979). The bumble-bee visits mainly a certain flower type, the major one, but once in a while it samples (doing minoring) other flower types. It would be interesting to investigate how an individual bee's parameter ϵ is influenced by its life history and its environment.

Milinski (1984) and Godin & Keenleside (1984) obtained interesting results when comparing the switching rate between two resources of fish with different competitive ability: individuals experiencing a high feeding rate (high payoff) tend to switch patches less frequently than those individuals that received lower payoffs. These results can be explained by our ϵ-sampling strategy (and also by the failures strategy). The fishes which are receiving less, reach the threshold of leaving more frequently, and the initiative to sample somewhere else is greater when ϵ-sampling is payoff-dependent (with ϵ increasing with low payoffs and decreasing with high payoffs).

ATTITUDE TOWARDS RISK

Our model explains in a simple way (without the need of utility theory) the well-known pattern in animal behavior of risk aversion and risk proneness (Real & Caraco, 1986; Stephens & Krebs, 1986; Krebs & Kacelnik, 1991; McNamara & Houston, 1992): in an environment in which the resource is normally distributed, the critical level can be interpreted as an existing condition for the animal. If the critical level is below the resource mean (Fig. 2), then the animals should behave as if they are risk-averse, while if the critical level is above the mean, then they should behave as if they are risk-prone. Our model predicts only a tendency to visit one of the resources more frequently and not to make an exclusive choice for one of the resources. In the case where nectar is distributed as in Fig. 3: no matter what its critical level is, the bee will prefer the blue flower.

The elucidated review on risk sensitivity by McNamara & Houston (1992) has technically similar results to our points on attitude towards risk. However, they ask themselves which alternative the animal would prefer, while we find out what would happen to the animal if we take into account the observations of the IFD and matching. In their model the critical level is a kind of evolutionary knowledge which, in a sense uses complete information about the environment. In our model the animal's actions are governed only by its own recent experiences and no complete information is required.

BOUNDED RATIONALITY AND MYOPIC LEARNING

Our approach to studying foraging behavior is quite different from the "optimal foraging theory" used in ecology (Pyke *et al*., 1977; Krebs & Kacelnik, 1991; Stephens & Krebs, 1986; Bernstein *et al*., 1988). In optimal foraging theory, the decision to leave a patch (resource alternative) is based on a comparison to the surroundings; in other words, it assumes that the animal has complete information and a powerful memory and computational ability. Our basic approach is that the animal uses "bounded memory" and makes its decisions only on the basis of its own recent experience. It does not know its competitor's moves/payoffs. It even may not know that it is involved in a game situation. The animal uses very simple decision rules to decide when to leave a patch (flower type), to decide where to go, and to decide whether or not to stay at the "new" patch. In such very fast biological activities (one bee makes very many visits per minute) the animals mainly use their short-term memory (Menzel, 1985, 1990) and the movement rules depend on very short recall (e.g. remember the last one to three flowers) and very simple calculations (Real *et al*., 1990; Real, 1991, 1992).

These issues are related to myopic learning models (Monderer & Shapley, 1988; Fudenberg & Kreps,

1991; Milgrom & Roberts, 1991; Monderer & Sela, 1993) and to theory on bounded rationality (Kalai, 1990; Selten, 1990; Aumann, 1992). We believe that bees and most other animals are not able to perform sophisticated calculation of probabilities (e.g. as in the RPS-rule of Harley, 1981, the learning rule by McNamara & Houston, 1985, or in learning rules that require Bayesian updating) and cannot update expected payoffs by functions that comprise a long recall. Of course, in a matching experiment the reward probabilities are not known to the bee; these are known only to the researcher. One of the main limitations of many of the previous models is that they analyze the situation as if the bee knows those probabilities.

This bounded rationality approach is explained nicely in Boyd & Richerson (1985: 93) when they address the issue of how animals and people apply Bayesian rationality:

simple rules of thumb (… called heuristics by psychologists) may greatly reduce cognitive complexity of decisions but still result in behavior that closely approximates normatively rational behavior in some restricted range of environments … These heuristics often work well but occasionally lead to behavior that is irrational according to canons of Bayesian rationality.

In this paper we have presented an explicit model in which simple decision rules, which need only very short recall and only elementary calculations, can dictate an optimal foraging strategy. We have seen that finite automata with very few states appear to be appropriate tools for such tasks (Ben-Porath, 1991; Ben-Porath & Peleg, 1987). Our model stands in agreement with recent experiments of foraging animals which reveal that animals take into account only the last one to three rewards when making short-term decisions (*sensu* Menzel, 1990). It also fits the "melioration approach" (Herrenstein & Vaughan, 1980) that animals use very simple choice rules which lead them to behave (sub)optimally in very complex natural situations (Houston *et al*., 1982; Hinson & Staddon, 1983; and Boyd & Richerson, 1985). To an outside observer this simple behavior looks very sophisticated and complicated—as if they use utility functions, probability updating and complicated calculus. We believe that the same approach can explain some "irrational" behavior in economics and sociology; some "bounded rational"—*ad hoc*—strategies that are optimal under particular natural conditions may look very irrational in artificial situations. This is illustrated by the comparison of the matching experimental and the IFD phenomenon in nature.

REFERENCES

AUMANN, R. J. (1992). Irrationality in game theory. In: *Economic Analysis of Markets and Games*, *Essays in Honor of Frank Hahn* (Dasgupta, P., Gale, D., Hart O. & Maskin, E. eds). pp. 214–227. Cambridge: MIT Press.

BEN-PORATH, E. (1991). Repeated games with finite automata. Working paper No. 7, The Suckler Institute of Economic Studies, Tel Aviv University.

BEN-PORATH, E. & PELEG, B. (1987). On the folk theorem and finite automata. Mimeo, Center for Research in Mathematical Economics and Game theory.

BERNSTEIN, C., KACELNIK, A. & KREBS, J. R. (1988). Individual decisions and the distribution of predators in a patchy environment. *J. Anim. Ecol*. **57,** 1007–1026.

BOKER, G. (1993). Pollination ecology of Eremostachys laciniata (Lamiatceae). M.Sc. Thesis, Dept. of Horticulture, Faculty of Agriculture, Hebrew University of Jerusalem.

BOYD, R. & RICHERSON, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.

BUSH, R. R. & MOSTELLER, F. (1955). *Stochastic Models for Learning*. New York: Wiley.

COMMONS, M. L., HERRENSTEIN, R. J. & RACHLIN, H. (1982). *Quantitative Analysis of Behavior*, *Vol. 2. Matching and Maximizing Accounts*. Cambridge, MA: Ballinger.

CRESSWELL, J. E. (1990). How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamon Monarda fistulosa (Lamiaceae)? *Oecologia* **82,** 450–460.

DAVISON, M. & MCCARTHY, D. (1988). *The Matching Law*. Hillsdale, NJ: Lawrence Erlbaum Associates.

DEGROOT, M. (1970). *Optimal Statistical Decisions*. New York: McGraw-Hill.

FISHBURN, P. C. (1976). Continua of stochastic dominance relations for bounded probability distributions. *J. Math. Econ*. **3,** 295–312.

FRETWELL, S. D. (1972). *Seasonal Environments*. Princeton, NJ: Princeton University Press.

FRIEDMAN, J. & SHMIDA, A. (1992). Pollination, gathering nectar, and the distribution of flower species. Discussion paper no. 14, Center for Rationality, The Hebrew University of Jerusalem.

FUDENBERG, D. & KREPS, D. (1991). Learning and equilibrium in games. Mimeo, MIT.

GODIN, J. G. & KEENLESIDE, M. H. A. (1984). Foraging on patchily distributed prey by a cichlid fish: a test of the Ideal Free Distribution theory. *Anim. Behav*. **32,** 120–131.

HAMMERSTEIN, P. & SELTEN, R. (1993). Evolutionary game theory. In: *Handbook of Game Theory with Economic Applications* (Aumann R. J. & Hart, S. eds). Amsterdam: North-Holland.

HARDER, L. D. (1987). Choice of individual flowers by bumble bees: interaction of morphology, time and energy. *Behaviour* **104,** 60–77.

HARLEY, C. B. (1981). Learning the evolutionary stable strategy. *J. theor. Biol*. **89,** 611–633.

HEINRICH, B. (1979). *Bumblebee Economics*. Cambridge, MA. Harvard University Press.

HERRENSTEIN, R. J. (1970). On the law of effect. *J. expl Anal. Behav*. **13,** 243–266.

HERRENSTEIN, R.J. & VAUGHAN, W. Jr. (1980). Melioration and behavioral allocation. In: *Limits to Action* (Staddon, J. E. R., ed.). New York: Academic Press.

HEYMAN, G. M. (1979). Markov model description of changeover

probabilities on concurrent variable interval schedules. *J. expl Anal. Behav*. **31,** 41–51.

HINSON, J. M. & STADDON, J. E. R. (1983). Hill-climbing by pigeons. *J. expl Ana. Behav*. **39,** 25–47.

HOUSTON, A. I. (1983). Optimality theory and matching. *Behav. Anal. Lett*. **3,** 1–15.

HOUSTON, A. I., KACELNIK A. & MCNAMARA, J. M. (1982). Some learning rules for acquiring information. In: *Functional Ontogeny* (McFarland, D. J., ed.). New York: Pitman.

HOUSTON, A. I. & MCNAMARA, J. M. (1986). Switching between resources and the ideal free distribution. *Anim. Behav*. **35,** 301–302.

HOUSTON, J. M. & SUMIDA, B. H. (1987). Learning rules, matching and frequency dependence. *J. theor. Biol*. **126,** 289–308.

KADMON, R. & SHMIDA, A. (1992). Departure rules used by bees foraging for nectar: A field test. *Evol. Ecol*. **6,** 142–151.

KADMON, R., SHMIDA, A. & SELTEN, R. (1992). Within-plant foraging behavior of bees and its relationship to nectar distribution in Anchusa strigosa. *Isr. J. Bot*. **40,** 283–294.

KALAI, E. (1990). Bounded rationality and strategic complexity in repeated games. In: *Game Theory and Applications* (Ichiishi, T., Neyman, A., & Tauman, Y., eds). pp. 131–157. New York: Academic Press.

KREBS, J. R., KACELNIK, A. & TAYLOR, P. (1978). Test of optimal sampling by foraging great tits. *Nature* **275,** 27–31.

KREBS, J. R. & KACELNIK, A. (1991). Decision-making. In: *Behavioural Ecology* (Krebs, J. R. & Davies, N. B. eds). pp. 105–136. London: Blackwell Scientific.

LAVERTY, T. M. (1980). The flower-visiting behavior of bumble bees: floral complexity and learning. *Can. J. Zool*. **58,** 1324–1335.

MAYNARD SMITH, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

MAYNARD SMITH, J. (1984). Game theory and the evolution of behavior. *Behav. Brain Sci*. **7,** 95–125.

MCNAMARA, J. M. & HOUSTON, A. I. (1985). Optimal foraging and learning. *J. theor. Biol*. **117,** 231–249.

MCNAMARA, J. M. & HOUSTON, A. I. (1992). Risk-sensitive foraging: A review of the theory. *Bull. Math. Biol*. **54,** 355–378.

MENZEL, R. (1985). Learning in honey bees in an ecological and behavioral context. In: *Experimental Behavioral Ecology* (Holldobler & Lindauer, eds). pp. 55–73. Stuttgart: G. Fischer Verlag.

MENZEL, R. (1990). Learning, memory and "cognition" in honey bees. In: *Neurobiology of Comparative Cognition* (Kesner, R. P. & Olten, D. S. eds). pp. 237–292. Hillsdale, NJ: Erlbaum.

MENZEL, R. & GREGGER, U. (1992). Temporal dynamics and foraging behavior in honeybees: In: *Biology and Evolution of Social Insects* (Billen, J. ed.). pp. 303–318. Leuven, Belgium: Leuven University Press.

MENZEL, R. & SHMIDA, A. (1992). The ecology of flower colors and the natural color vision systems of insect pollinators. *Biol. Rev*. **68,** 81–120.

MILGROM, P. & ROBERTS, J. (1991). Adaptive and sophisticated learning in repeated normal form games. *Games Econ. Behav*. **3,** 82–100.

MILINSKI, M. (1979). An evolutionary stable feeding strategy in sticklebacks. *Z. Tierpsychol*. **51,** 36–40.

MILINSKI, M. (1984). Competitive resource sharing: an experimental test of a learning rule for ESS's. *Anim. Behav*. **32,** 233–242.

MILINSKI, M. & PARKER, G. (1991). Competition for resources. In: *Behavioral Ecology* (Krebs, J. R. & Davies, N. B., eds). pp. 137–168. Oxford: Blackwell Scientific.

MONDERER, D. & SHAPLEY, L. S. (1988). Potential games. Mimeo, The Technion, Haifa.

MONDERER, D. & SELA, A. (1993). Fictitious play and no-cycling conditions. Mimeo, The Technion, Haifa.

MOTRO, U. & SHMIDA, A. (1995). Near–far search: an evolutionary stable foraging strategy. *J. theor. Biol*. **173,** 15–22.

NEYMAN, A. (1985). Bounded complexity justifies cooperation in the finitely repeated prisoner's dilemma. *Econ. Lett*. **19,** 227–230.

PARKER, G. A. & SUTHERLAND, W. J. (1986). Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim. Behav*. **34,** 1222–1242.

PELEG, B. & SHMIDA, A. (1992). Short-run stable matchings between bees and flowers. *Games Econ. Behav*. **4,** 232–251.

PYKE, G. H., PULLIAM, H. R. & CHARNOV, E. L. (1977). Optimal foraging: A selective review of theory and tests. *Q. Rev. Biol*. **52,** 137–154.

REAL, L. A. (1991). Animal choice behavior and the evolution of cognitive architecture. *Science* **253,** 980–986.

REAL, L. A. (1992). Information processing and evolutionary ecology of cognitive architecture. *Am. Nat*. **140,** S108–S145.

REAL, L. & CARACO, T. (1986). Risk and foraging in stochastic environments. *A. Rev. Ecol. Syst*. **17,** 371–390.

REAL, L. A., ELLNER S. & HARDER, L. D. (1990). Short-term energy maximization and risk-aversion in bumble bees: A reply to Possingham *et al*. *Ecology* **71,** 1625–1628.

ROTHSCHILD, M. (1974). A two-armed bandit theory of market pricing. *J. Econ. Theor*. **9,** 185–202.

SELTEN, R. (1975). Re-examination of the perfectness concept for equilibrium points in extensive games. *Int. J. Game Theor*. **4,** 25–55.

SELTEN, R. (1978). A model of oligopolistic size structure profitability. *Eur. Econ. Rev*. **12,** 1–24.

SELTEN, R. (1990). Bounded rationality. *J. Instit. Theor. Econ*. **146,** 649–658.

SHMIDA, A., O'TOOLE, C. & IVRI, Y. (1993). Elements of bee-flower pollination market in Israel. Mimeo, Dept. of Ecology and Evolution, The Hebrew University of Jerusalem.

SHREIBER, E. (1993). Foraging strategies in carpet inflorescences of Alkanna strigosa (Boraginaceae) by solitary bees. M.Sc. Thesis, Dept. of Ecology and Evolution, The Hebrew University of Jerusalem.

SIMON, H. A. (1956). A comparison of game theory and learning theory. *Psychometrika* **21,** 267–272.

STADDON, J. E. R. (1983). *Adaptive Behavior and Learning*. Cambridge: Cambridge University Press.

STADDON, J. E. R. & HORNER, J. M. (1989). Stochastic choice models: A comparison between Bush-Mosteller and a source-independent reward-following model. *J. expl. Anal. Behav*. **52,** 57–64.

STEPHENS, D. W. & KREBS, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.